COMPARATIVE ANATOMY AND SYSTEMATICS OF MOUTABEAE (POLYGALACEAE)*

CHARLES H. STYER

THE POLYGALACEAE, as now generally constituted, contain three tribes: Polygaleae, Xanthophylleae, and Moutabeae (van Royen & van Steenis, 1952; Scholz, 1964; Hutchinson, 1967). However, their generic constitution and ordinal position have proven problematical. The genera which have been shifted in and out of the family most frequently are *Xanthophyllum* Roxb. (Wettstein, 1935; Dube, 1962; Cronquist, 1968) and *Diclidanthera* Mart. (Miers, 1861; Gürke, 1891; Chodat, 1896; Perkins, 1907; Gilg, 1908; Engler & Gilg, 1924; Sprague, 1940; O'Donell, 1941; Pittier, 1942; Erdtman, 1944; Metcalfe & Chalk, 1950). In addition, the affinities of *Barnhartia* Gleason (Gleason, 1926) and *Moutabea* Aublet (Endlicher, 1839) have not been clear. This study of the vegetative anatomy of members of the tribe Moutabeae was undertaken to clarify the relationships of the taxa of this group.

DESCRIPTIONS AND DISTRIBUTIONS

Polygalaceae tribe **Moutabeae** Chodat (1896). Shrubs, lianas, or trees. Leaves alternate, simple, entire. Calyx and corolla united at the base (a feature which separates the Moutabeae from the other tribes of the Polygalaceae), calyx gamosepalous, corolla polypetalous to gamopetalous. Stamens 7, 8, or 10, monadelphous or subdiadelphous, or free and adnate to free petals; anthers dehiscing by a slit. Ovary syncarpous, 2–8-locular, with 1 ovule per locule. Three genera with ca. 19 species in South America and Panama; one monotypic genus in New Guinea and the Solomon Islands (van Royen & van Steenis, 1952; Hutchinson, 1967).

1. **Barnhartia** Gleason (1926). Liana growing to the tops of trees. Inflorescence a leafy, axillary or terminal panicle; flowers subzygomorphic; sepals and petals 5; petals connivent, not fused, with orange claws and maroon blades; stamens 7–8, adnate to petals; ovary 2- or 3-locular; apex of petiole with glands. One species, *B. floribunda*. Guyana, Surinam, Brazil, and Venezuela.

2. **Diclidanthera** Martius (1827). Small trees or lianas. Inflorescence a terminal or axillary raceme or panicle; calyx 5-lobed; corolla tube 5-lobed and white; stamens 8 or 10, monadelphous; anthers glabrous; ovary 5-locular. About 8 species. Brazil, Venezuela, Colombia, and Peru.

* Scientific article no. A2290, contribution no. 5288, of the Maryland Agricultural Experiment Station.

3. **Eriandra** van Royen & van Steenis (1952). Tree to 80 feet. Inflorescence a small, few-flowered axillary raceme; flowers white, scented; sepals 4–5; petals 4–5, free at apex only; stamens 8 or 10, monadelphous; anthers densely pubescent; ovary 7–8-locular. One species, *E. fragrans*. Solomon Islands and New Guinea.

4. **Moutabea** Aublet (1775). Tree to 35 feet, shrubs or lianas. Inflorescence a short axillary raceme; flowers strongly zygomorphic; sepals and petals 5; corolla tubular; stamens 7 or 8, diadelphous; ovary 4–5-locular; seed without endosperm. About 10 species. Brazil, French Guiana, Guyana, Venezuela, Colombia, Peru, and Panama.

TAXONOMIC HISTORY

Moutabea was described by Aublet in 1775 and was placed among the Monadelphia, Pentandria. Endlicher (1839) listed *Moutabea* among the *genera dubiae affinitatis* at the end of his ordo Ebenaceae, while Lindley (1846) placed it in the Polygalaceae. Miquel (1856) treated *Moutabea* as a member of the Ebenaceae, although in his discussion of its placement, he suggested that it belonged in the Polygalaceae. For the most part, Lindley's placement of *Moutabea* in the Polygalaceae has been followed to the present day. Chodat (1896) established the tribe Moutabeae in which he included only *Moutabea*.

Diclidanthera was named and described by Martius in 1827, and was placed in the Ebenaceae. Reichenbach (1828) listed *Diclidanthera* among the Styraceae which, in turn, were listed under the family Sapotaceae. Reichenbach's placement of *Diclidanthera* among the Styraceae was accepted by many botanists. It is interesting that Reichenbach also included *Moutabea* in the Sapotaceae; therefore, almost immediately after the description of *Diclidanthera* it was tenously linked with *Moutabea*. Lindley (1836) listed *Diclidanthera* under his Styraceae, which he tentatively positioned as a suborder of the Ebenaceae. Endlicher's (1839) disposition of the genus was similar. More recently, Bentham (1876) and Gürke (1891) also included *Diclidanthera* in the Styracaceae.

Other authors disagreed with the treatments noted above. De Candolle (1844) enumerated several ways in which *Diclidanthera* differed from both the Styracaceae and the Ebenaceae. Perkins removed *Diclidanthera* from the Styracaceae in 1907, and although she had no suggestions for its proper position, it was not again treated as a member of that family. Gilg (1908) agreed with Perkins and assigned *Diclidanthera* to its own family, the Diclidantheraceae; this usage has been followed by some until recently (Wettstein, 1935; Engler & Diels, 1936; Metcalfe & Chalk, 1950). Gilg, however, had been anticipated by Agardh, who published the Diclidantheraceae in 1858. Thus, Diclidantheraceae Gilg is a later homonym of Diclidantheraceae Agardh. Miers (1861) first thought *Diclidanthera* was hamamelidaceous but later changed his mind and placed it in the Byttneriaceae. He wrote that ". . . *Diclidanthera* bears little relation toward the

Ebenaceae, Styraceae or Polygalaceae . . . ," indicating that some botanists had found a place for *Diclidanthera* in the Polygalaceae, as Miquel (1856) and Martius (von Mohl & von Schlechtendal, 1856) had indeed suggested.

Miquel's and Martius's belief that *Diclidanthera* should be placed in the Polygalaceae was greatly strengthened by two quite unrelated events. First, Gleason (1926) described a new genus, *Barnhartia*, which was soon shown (Sprague & Sandwith, 1932; Sprague, 1940) to be intermediate in floral structure between *Diclidanthera* and *Polygala*, thus linking *Diclidanthera* to the Polygalaceae. The second important occurrence was associated with botanists' growing awareness of the necessity to study as many characters as possible when determining the affinities of troublesome plants. In this case, *Diclidanthera* pollen was shown to be ". . . of a type peculiar to the Polygalaceae . . ." (Sprague, 1940), a fact confirmed by Erdtman (1944, 1952). Once *Diclidanthera* was shown to be a member of the Polygalaceae, the fusion of its sepals and petals into a tube made its affinity to *Moutabea* and its placement in the tribe Moutabeae obvious. The position of *Diclidanthera* in the Moutabeae is supported by the observation that all Moutabeae (*Moutabea*, *Diclidanthera*, *Barnhartia*, and *Eriandra*) appear to be aluminum accumulators (Chenery, 1948; van Royen & van Steenis, 1952; Hegnauer, 1969).

It is interesting to note, despite the various treatments of *Diclidanthera* and *Moutabea*, that ever since Reichenbach first indicated an affinity between them, these two genera have often been placed near each other in taxonomic studies (Lindley, 1836; Endlicher, 1839; Miquel, 1856; von Mohl & von Schlechtendal, 1856; De Candolle, 1873). However, it was not until the discovery of *Barnhartia* that this affinity was clarified.

Gleason described *Barnhartia* in 1926. He thought that its floral structure indicated a relationship with the Styracaceae, but also noted a likeness to *Diclidanthera*. He commented that Perkins had excluded *Diclidanthera* from the Styracaceae, thus leaving the position of his new genus in question. As mentioned above, Sprague and Sandwith (1932) saw the importance of *Barnhartia* as a link between *Polygala* and *Diclidanthera*. Thus, *Barnhartia*, *Diclidanthera*, and *Moutabea* (which Martius had suggested was closely related to *Diclidanthera*) all came to be associated in the Moutabeae.

The last genus to be placed in the Moutabeae was *Eriandra*, described by van Royen and van Steenis in 1952. Although *Eriandra* was from New Guinea and not South America (as were other members of the tribe), thus creating what the authors considered a "most remarkable" distribution, van Royen and van Steenis were convinced *Eriandra* was ". . . closely related to *Diclidanthera*, *Moutabea*, and *Barnhartia*."

Members of the Moutabeae are of little economic importance. Record and Hess (1943) list *Moutabea* in their *Timbers of the New World*, but give no uses, mentioning only that it is a climber. However, several common names (graine macaque, aymoutabou, caimito do monte, gogo de guariba, graõs de macaco) exist for *Moutabea*, indicating local familiarity and per-

haps some economic importance (Aublet, 1775; Oort, 1939; Record & Hess, 1943). *Moutabea* fruit is said to be edible (Macbride, 1950; Lewis & Herrera-MacBryde, 1969). A herbarium label (*Forest Department of British Guiana 3015*) states that the stem of *Barnhartia* makes "a strong rope used for stringing timbers from ballahoos [schooners with the foremast raking forward and the mainmast aft]."

ANATOMICAL REVIEW

Metcalfe and Chalk (1950) stated that "the anatomy of the Brazilian shrubs and trees belonging to the genus *Diclidanthera* is rather imperfectly known." The same may be said for the other three genera of Moutabeae. Only passing references to anatomical information are available for *Eriandra* (van Royen and van Steenis, 1952) and *Barnhartia* (Metcalfe & Chalk, 1950; Sprague, 1940).

In their summary of the anatomy of *Diclidanthera*, Metcalfe and Chalk (1950) noted that the dorsiventral leaf has hairs divided by thin septa, a hypoderm of 1 to 2 layers below the upper epidermis, and a palisade layer about 3 cells thick. Veins are sheathed by thick-walled fibers, and numerous crystals occur in cells adjacent to these fibers. Based on O'Donell (1941), their description of the wood noted mostly solitary vessels with simple perforations and alternate intervascular pitting, vasicentric parenchyma, heterogeneous rays of types IIA and IIB (Kribs, 1935), and fibers with large bordered pits. Metcalfe and Chalk also mentioned anomalous secondary thickening in the stem. Solereder (1908), Gürke (1891), and Erdtman (1944) have also made contributions to the anatomical studies of *Diclidanthera*.

The anatomy of *Moutabea* has probably received more attention than that of any other member of the tribe. Unfortunately, most of this work has been in conjunction with broad surveys which did not include detailed generic descriptions, although specific details were occasionally noted. For instance, Metcalfe and Chalk (1950) included *Moutabea* in their treatment of the Polygalaceae and only the following facts can be applied with certainty to *Moutabea* leaves: they are dorsiventral; the epidermal cells have straight anticlinal walls; a hypoderm and long sclerosed cells in the palisade layer are present in *M. guianensis*; the midrib is two-stranded, the upper strand of which is inverted. A small amount of additional information is available on *Moutabea* in Erdtman (1944) and Foster (1947). More information is available on the wood anatomy of *Moutabea* than on the leaf anatomy. Wood anatomy may be summarized as follows: pores are solitary, scattered, large or occasionally small; tyloses may be present; intervascular pits are medium to coarse; vessel to ray pit-pairs are half-bordered; rays are heterogeneous (Kribs Type IIA, 1935) and 6–8 cells wide; axial xylem parenchyma is diffuse-in-aggregates and scanty paratracheal (Metcalfe & Chalk, 1950; Record & Hess, 1943; Biswas, 1969; Heimsch, 1942).

Although several papers have dealt with anomalous growth in polygala-

ceous lianas (Crüger, 1850; Müller, 1866; Schenck, 1893; Pfeiffer, 1925, 1926), these have usually given descriptions and illustrations of genera in the Polygaleae, mainly *Securidaca.* Chodat (1896) described anomalous growth in *Moutabea* as being formed by half-moon- or sickle-shaped segments of xylem which are added onto the central cylinder. Pfeiffer (1926) wrote that anomalous growth in *Moutabea* is of the concentric stem type (*corpus lignosum circumvallatum*). Meristematic action which forms this type of anomaly was attributed by Chalk and Chattaway (1937) to a short-lived cambium, replaced periodically by new meristematic tissue originating either in the pericycle or the cortex which repeats the structure of the young stem. De Bary (1884), however, believed that new cambia originated in the "bast-zone."

MATERIALS AND METHODS

Specimens studied in this investigation are documented in TABLE 1. With the exception of several prepared slides obtained from Jodrell Laboratory, Royal Botanic Gardens, Kew, and fluid-preserved leaves and wood of *Moutabea guianensis* Aublet, all specimens were dried, either leaves from herbarium sheets or dried wood samples.

Standard techniques were used in preparing these materials for study. The dry wood samples were boiled in an "Aerosol OT" solution in a reflux apparatus for periods of up to four days in order to rehydrate and soften the wood. (This procedure is a modification by Rock (1972) of a technique outlined by Ayensu (1967).) Fluid-preserved wood was not treated in this way prior to embedding. Following embedding in celloidin, the material was stored in a 1:1 solution of glycerin and 95% ethanol. Transverse, radial, and tangential sections were cut on a sliding microtome, stained in Heidenhain's iron-alum haematoxylin, counter-stained with safranin, dehydrated, and mounted in Canada balsam.

Macerations were prepared following a variation of Jeffrey's method (Rock, 1972).

Dry leaves were boiled briefly in water to rehydrate them. Fluid-preserved leaves were not so treated. Clearings were prepared using a modification of Arnott's (1959) technique. Leaves were first treated with 5% NaOH, washed in water, immersed in Stockwell's solution (Johansen, 1940), washed in water again, then immersed in chloral hydrate. After a final washing, the leaves were stained in safranin, dehydrated, and mounted in Canada balsam. Because the large number of sclereids in some species of *Moutabea* rendered the clearing process ineffective, additional preparations of some of this material were prepared in the following manner: after the final wash of the clearing process, the lower epidermis was stripped away, stained in safranin, dehydrated, and mounted in Harleco Synthetic Resin (HSR). The sclereids were then scraped off the remaining piece of leaf, stained in safranin, dehydrated, and mounted in HSR.

Transverse and paradermal sections of leaves were prepared from material embedded in paraffin. Sections were cut at 10 micrometers (μm.) on

TABLE 1. **Specimens of Moutabeae examined.**

SPECIES [1]	COLLECTOR [2]	COLLECTION LOCALITY	HERBARIUM [3]	XYLARIUM [4]	LEAF	WOOD	SLIDES [5]
Barnhartia floribunda Gleason	Boschwezen 6707	Surinam	U		+		
	L.B.B./Boerboom 8732	Surinam	BBS		+		
	de la Cruz 2727	British Guiana	NY		+		
	Sandwith 507	British Guiana	NY	K–JW			l, t
Diclidanthera bolivarensis Pittier	Wurdack & Monachino 41332	Venezuela	US		+		
Diclidanthera elliptica Miers	Hoehne 28421	Brazil	NY, US		+		
Diclidanthera laurifolia Martius	Mexia 5141	Brazil	NY, US	K–JW	+		l, t
	Riedel 1158	Brazil	U, NY		+		
Diclidanthera octandra Gleason	Froés 24037	Brazil	US		+		
Diclidanthera penduliflora Martius	Murça Pires & Black 1727a	Brazil	US		+		
	Spruce 1030			K–JW			l, t
Eriandra fragrans van Royen & van Steenis	Boschwezen 5810	West Irian, New Guinea		FPAW		+	
	C. Koster (Boschwezen 8062)	West Irian, New Guinea	FPA, L	FPAW	+	+	
Eriandra fragrans van Royen & van Steenis	Boschwezen 11903	New Guinea	L	LW		+	
	Pullen 1151	New Guinea	L	FPAW	+	+	
	F. C. Whitmore (British Solomon Islands Protectorate 1413)	Solomon Islands	L		+		
Moutabea aculeata (Ruiz & Pavon) Poeppig & Endlicher	Klug 3936	Peru	US, NY		+		
Moutabea excoriata Martius ex Miquel	Smith 4674	Brazil	US		+		
Moutabea guianensis Aublet	Pulle 389	Surinam	L, U	UW 6498	+	+	
	Murça Pires *s.n.*	Brazil	T [6]		+ [7]	+ [7]	
	Van Donselaar 3193	Surinam	U	UW 12022	+	+	
Moutabea longifolia Poeppig & Endlicher	Krukoff 7056	Brazil	US, NY	AW 37053, PRFW		+	
	Froés 11709	Brazil	NY		+		
Moutabea sp.	Wurdack & Adderly 43409	Brazil	US	USW 17988	+	+	

[1] Names used are those originally associated with specimens.
[2] If the collector is unknown or if he did not number the specimen, the collection is identified by an institutional number.
[3] Herbarium abbreviations follow those recommended by Holmgren and Keuken (1974) in *Index Herbariorum*, ed. 6.
[4] Xylarium abbreviations follow those recommended by Stern (1967) in *Index Xylariorum*.
[5] Prepared microscope slides from K–JW: l = leaf section; t = twig section.
[6] Murça Pires writes of this material: "It is the same species which has been collected by Archer [i.e., William Andrew Archer] and is represented at the U. S. National Herbarium (US): *Archer 7978, 8252, 8215, 7904.*"
[7] These represent the only fluid-preserved materials; all other materials were dried.

a rotary microtome, stained with Heidenhain's iron-alum haematoxylin and safranin, and mounted in HSR. Since the staining technique employed often dissolved out any crystals present (Stern *et al.*, 1970), one slide of each specimen was mounted unstained.

Diagnostic characters used in describing the woods were selected from those suggested by Tippo (1941) and Tamolang *et al.* (1963). Except for *Barnhartia* and *Diclidanthera*, where measurements were made from sections because the small bits of stem available precluded maceration, lengths of imperforate tracheary elements and vessel elements were measured from macerated material. Pore distribution, pore diameter, and vessel element end wall angle were measured from sectioned material. The total tip-to-tip length of vessel elements was recorded. Since ligules often are not visible in section, measurements of vessel element length made from sections probably resulted in lengths shorter than the true values. Tangential pore diameters were measured from middle lamella to middle lamella. End wall angles were measured in degrees with a goniometer eyepiece. Pore distribution was determined by counting the numbers of solitary pores, pore clusters, and radial pore multiples from ten random fields of view. The percentage of pore groupings for each class was computed by dividing the frequency for each class by the total frequency for all classes.

Photographs were prepared in two ways. Some were prepared by conventional photomicrography using an attachment camera on a Wild M-20 compound microscope. Other photographs were made by placing the specimen-containing microscope slide itself on the stage of a photographic enlarger and projecting an image of the specimen directly onto photographic paper; that is, the mounted specimen was used instead of a photographic negative. Magnifications of up to 16× were possible with a 50 mm. enlarging lens. A print made in this way has a negative image (FIGURES 1–5). The positive print seen in FIGURE 11 was obtained by making a contact print of the original negative print.

Diagnostic characters to be used in describing leaves were selected from Esau (1965) and developed through discussion with W. L. Stern. Length and diameter of stomatal apparatuses were measured either from clearings or from paradermal sections; cuticle thickness was measured from transverse sections.

Measurements were rounded according to the following schedule: 0–10 μm. to the nearest 0.1 μm., 11–100 μm. to the nearest 1 μm., above 100 μm. to the nearest 10 μm.

Terminology used in the description of woods follows that of Tamolang *et al.* (1963) and is largely in accord with that of the Committee on Nomenclature, the International Association of Wood Anatomists, *International Glossary of Terms Used in Wood Anatomy* (1957), except for the description of axial xylem parenchyma which follows Hess (1950). Hess's categories of axial xylem parenchyma seemed more suited to the situation in Moutabeae than did those of other systems.

One arrangement of axial parenchyma found in Moutabeae is not in-

cluded in any of the usual groupings. This arrangement here termed "paratracheal diffuse with wings," resembles aliform parenchyma, but cannot be included in that category since the parenchyma does not completely surround the vessels. Furthermore, the wings are not solid parenchyma, but have imperforate tracheary elements scattered through them (FIGURE 9).

Bailey (1936) stressed the likelihood of finding genera with transitional series of cells between tracheids and fiber-tracheids, or between fiber-tracheids and libriform wood fibers. The former transition is present in Moutabeae, where imperforate tracheary elements vary from thin-walled, blunt-ended tracheids with pits of the same magnitude as intervascular pits, to thicker-walled, tapered fiber-tracheids with small bordered pits. The distinction between tracheid and fiber-tracheid is particularly hard to define in the Moutabeae because the vessel elements, and consequently the intervascular pits, vary greatly in size, making comparisons of pit borders difficult.

Growth rings which encircle the whole stem are absent in Moutabeae. However, faint, partial rings spanning short arcs are present and are termed "growth arcs." The ground mass of xylem, excluding conjunctive parenchyma and included phloem, is for convenience termed "normal xylem." The term "pithlike" is strictly descriptive and implies nothing about the origin or function of the tissue.

Terminology of leaf anatomy follows Esau (1965); terms for leaf architecture are based on Hickey (1973). Application of the terms "biseriate," "triseriate," or "multiseriate" to leaf epidermal structure is purely descriptive and does not imply ontogenetic derivation.

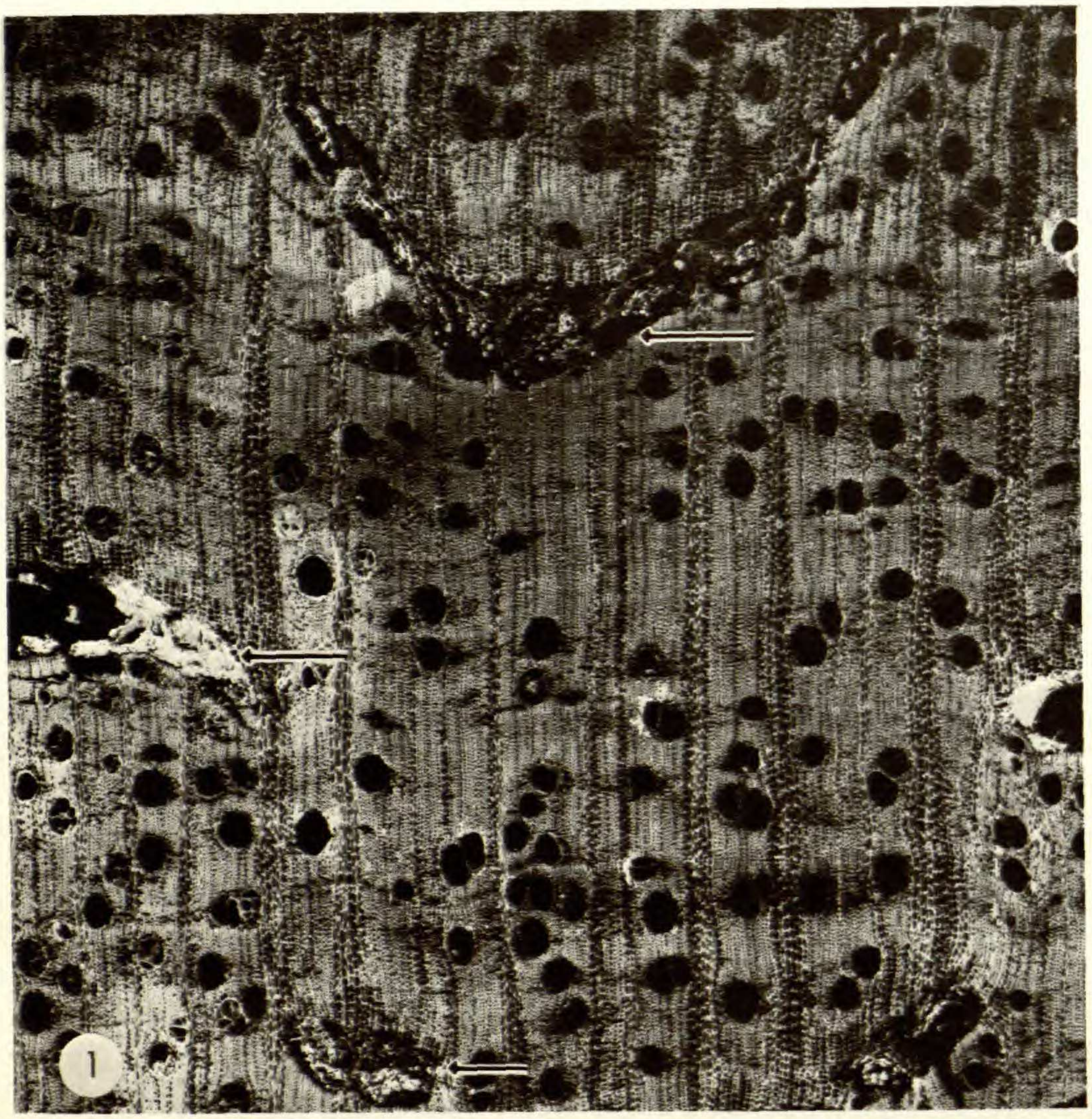
In citing literature, when the date of actual publication is different from that found on the title page of a book, that given in Stafleu's *Taxonomic Literature* (1967) has been accepted.

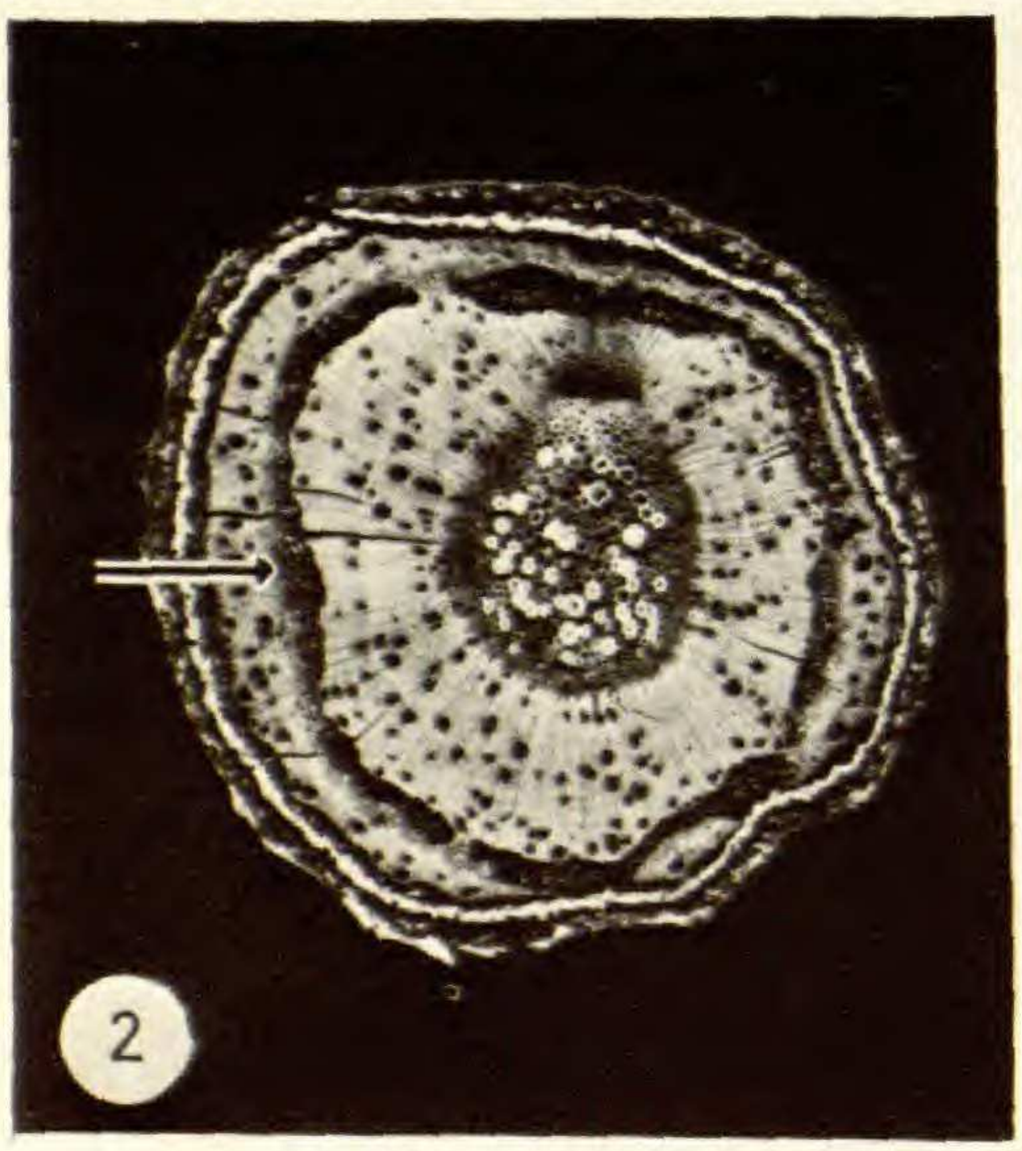
ANATOMY

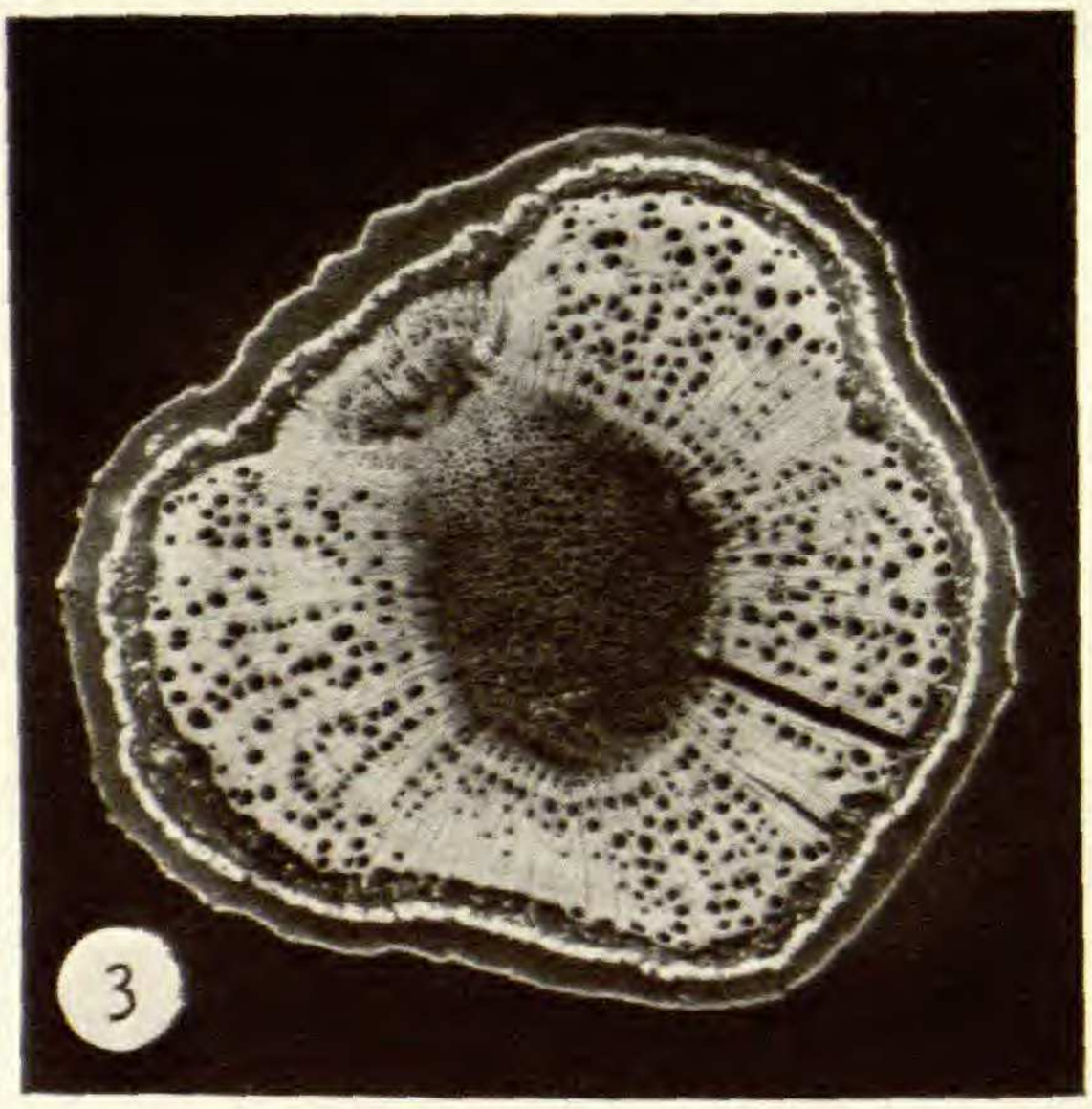
Barnhartia floribunda

WOOD. Wood for study of this genus was unsatisfactory because twigs taken from herbarium specimens do not show mature structure. However, comparison with similar material of other genera in the Moutabeae gives some insight into similarities and differences among these genera.

Growth arcs are absent. Pores are of fairly uniform size throughout the wood (FIGURE 3). Distribution of pore groups is 97.4% solitary and 2.6% radial multiples. Pore outline is circular or slightly angular in some of the narrower vessels. Vessel wall thickness varies from 1.4 to 2.7 μm. Tangential pore diameter averages 48 μm., with a range of 20 to 82 μm. Perforation plates are exclusively simple, generally with round perforations having only a very slight border. Tyloses are absent. Vessel element length (measured from sections) averages 410 μm., with a range of 160 to 580 μm. Intervascular pitting is alternate and pits are circular-bordered. Diameter of the pit border ranges from 6.8 to 8.1 μm. Inner







FIGURES 1–3: 1, *Eriandra fragrans*, transverse section of stem showing distribution of included phloem (arrows), × 12; 2, *Diclidanthera laurifolia*, transverse section of young stem showing first arc of included phloem (arrow), × 12; 3, *Barnhartia floribunda*, transverse section of young stem, × 12.

apertures are slitlike and crossed. Vessel element end wall angle ranges from 25° to 80°. Imperforate tracheary elements range from tracheids to fiber-tracheids. The pits are similar in shape to intervascular pits. Wall thickness ranges from 2.0 to 5.4 μm.

Vascular rays are both homocellular and heterocellular. Homocellular rays are nearly all uniseriate, ranging from 3.4 to 8.5 μm. wide and from 2 to 12 cells (54 to 450 μm.) high. All cells are erect. Heterocellular rays are mostly uniseriate and biseriate, but a few triseriate rays occur. Ray width varies from 8.5 to 24 μm., and height from 9 to 126 cells (220 to 3440 μm.). Cells of heterocellular rays range from procumbent to square or short erect cells, with tall erect cells forming uniseriate wings. Vessel to ray parenchyma pitting is half-bordered, the vessel side of the pit-pair having a circular border and a slitlike inner aperture, the ray side a simple pit corresponding to the border on the vessel side. No crystals or deposits occur in the ray parenchyma. Sheath cells are absent.

Axial xylem parenchyma is not abundant. A small amount of diffuse parenchyma is present, as well as some tangential parenchyma. Paratracheal diffuse parenchyma is also present. Vessel to axial xylem parenchyma pitting resembles vessel to ray pitting, i.e., pit-pairs are half-bordered with the circular border and slitlike inner aperture on the vessel side.

INCLUDED PHLOEM. No included phloem was observed (FIGURE 3).

LEAVES. *Barnhartia* leaves are simple and unlobed, with entire margins. Venation is pinnate; more specifically, brochidodromous. Areolation is mostly well developed and is partially oriented (see Hickey, 1973, for definition of terms). Veinlets are simple or branched, have clavate endings, and are not recurved. They consist of large, thin-walled, spirally thickened elements (probably tracheids) and are entirely surrounded by thin-walled bundle sheath cells.

Surfaces of *Barnhartia* leaves are more or less flat, and there are no unusual or pronounced topographic features.

Leaves are dorsiventral. The palisade layer usually consists of one full, complete layer, plus a second layer which is incomplete, considerable space occurring between adjacent palisade cells of the second layer. Sometimes a partial third layer is observed. One of the four samples studied differs considerably from this description. Sections of *Sandwith 507* possess a complete second palisade layer in which the cells are closely placed. Even the incomplete third layer is fairly extensive; the differences are heightened by the greater length of the palisade cells in the Sandwith collection than that observed in the other collections. Cells of the lower layer of the palisade in all collections are transitional with those of the subadjacent spongy layer. The configuration of the spongy mesophyll is modified slightly from the usual lacunose type because the branching of cells seems to be largely in the same plane as that of the blade, with few branches extending perpendicularly to this plane. This arrangement is most pronounced toward the abaxial side of the leaf.

Rhomboid and polyhedral crystals occur in abundance in the outermost

layer of bundle sheath cells. A small number of crystals occurs in the palisade cells next to the hypodermis and in the spongy cells next to the abaxial epidermis.

Except for the primary vein, vascular bundles of the leaves in *Barnhartia* consist of a single collateral bundle. The primary vein (as seen in transverse section) is more complex, consisting of a large area of xylem with phloem in round to oblong patches abaxial to it (FIGURE 12). In addition, there are one or two smaller areas of xylem adaxial to the large area of xylem and separated from it by a pithlike central region of parenchyma. This parenchyma is broken down in varying degrees, leaving small to large cavities next to the xylem (FIGURE 12, arrow). Possibly these cavities formed while the leaves were drying and are artifacts. The one or two smaller areas of xylem are flanked on their adaxial side by a variable thickness of phloem. Terminal veinlets lack phloem.

All veins except the terminal veinlets have a sheath of sclerenchyma between the vascular tissue and the bundle sheath. This sclerenchyma is widest in the primary vein and decreases in width with decreasing size of the vein; the smallest veinlets lack sclerenchyma altogether.

Bundle sheath cells are thickened on their radial and inner tangential walls, giving the bundle sheath the appearance very often seen in endodermides. Thickening of bundle sheath cells disappears in the smaller veins with the disappearance of the sclerenchyma sheath. The bundle sheath forms a continuous covering from the terminal veinlets to the primary vein. Bundle sheath extensions are absent.

The lower epidermis is uniseriate; the upper epidermis is largely triseriate. However, the number of epidermal layers over the primary vein may be as many as five, while in other areas of the blade the innermost epidermal layer is replaced by palisade cells.

In face view, the epidermal cells of both leaf surfaces are polygonal. The outer layer of the adaxial epidermis differs from the two inner layers in having smaller and mostly paired cells. Each pair is surrounded by a common, relatively thick cell wall, but is divided by a thin septum.

In sectional view, epidermal cells are square to rectangular. The cuticle is smooth-surfaced, varying in thickness from about 3 to 7 μm.

Stomata are restricted to the lower epidermis, where they are evenly distributed over the surface. The stomatal apparatus is anomocytic, no accessory cells being distinguishable. Guard cells are reniform; the pair roughly circular (length/width = 0.99). Guard cells are provided with a prominent outer cuticular ridge which projects beyond the surface of the leaf, as well as an inconspicuous inner ridge. In a median cross section of the guard cells, the periclinal walls are very heavily thickened, while the anticlinal walls are thin. No trichomes or hydathodes were observed.

Diclidanthera

WOOD. *Diclidanthera* wood was observed from slides prepared at the Jodrell Laboratory, Royal Botanic Gardens, Kew. These slides, prepared

from herbarium material, do not include mature wood. Only two species, *D. laurifolia* and *D. penduliflora*, were studied. Stems of the latter were represented only by transverse sections. Thus, pore distribution, pore diameter, pore outline, vessel wall thickness, and axial xylem parenchyma distribution represent the only combined data, since data requiring longitudinal sections could not be obtained for *D. penduliflora*.

Growth arcs, absent in *D. penduliflora*, are present in *D. laurifolia* (FIGURE 2). Pores are of uniform size distribution throughout. Distribution of pore groups is 88.7% solitary, 9.7% clusters, and 1.6% radial multiples in *D. penduliflora*; 98.1% solitary and 1.9% clusters in *D. laurifolia*. Pore outline is circular, with a slight angularity occurring in the narrower vessels. Vessel wall thickness varies from 2.0 to 4.1 μm. Tangential pore diameter averages 46 μm., with a range of 14 to 85 μm. Perforation plates are exclusively simple with essentially round perforations. Perforations have no (or only vestigial) borders. Tyloses are absent. Vessel element length (observed only in section) averaged 380 μm. and ranged from 210 to 580 μm. Intervascular pitting is alternate and circular-bordered. Pit-border diameter ranges from 5.4 to 6.8 μm. Inner apertures are slitlike and one half to three fourths the width of the border. End wall angle ranges from 10° to 89°. Imperforate tracheary elements range from tracheids to fiber-tracheids. Pits are the same shape as the intervascular pits. However, in elements most resembling fiber-tracheids, pits have longer inner apertures than do the intervascular pits. The longer inner apertures are positioned almost vertically in contrast to the almost horizontal apertures in the intervascular pitting. Wall thickness of imperforate tracheary elements ranges from 2.0 to 5.4 μm.

Vascular rays are both homocellular and heterocellular. Homocellular rays are mostly uniseriate, from 3.4 to 10.2 μm. wide, and consist of erect cells. Homocellular rays vary in height from 1 to 51 cells (48 to 1920 μm.). Heterocellular rays are usually uniseriate or biseriate. Ray width varies from 6.8 to 17 μm., and height from 3 to 53 cells (110 to 1950 μm.). The heterocellular rays consist of tall erect, square, and short procumbent cells. The tall erect cells often form uniseriate wings. Vessel to ray parenchyma pitting is half-bordered. Pits in vessel element walls have circular borders and slitlike inner apertures; those in ray cell walls are simple and coincide with the shape of the pit border in vessel element walls. No crystals or deposits occur in the ray parenchyma. Sheath cells are absent.

Axial xylem parenchyma is sparse; that which occurs is diffuse paratracheal. Vessel to axial parenchyma pitting resembles vessel to ray pitting. No crystals or deposits were observed.

INCLUDED PHLOEM. Included phloem occurs in the specimen of *D. laurifolia*, but not in that of *D. penduliflora*, possibly because of its immaturity. I suspect that older material would reveal the presence of included phloem in *D. penduliflora*. The included phloem of *D. laurifolia* contains sclereids, fibers, sieve tube elements, and axial parenchyma cells which contain crys-

FIGURE 4: *Eriandra fragrans*, radial section of stem, × 12.

tals. The arrangement of included phloem in *D. laurifolia* is shown in FIGURE 2.

LEAVES. *Diclidanthera* leaves are simple and unlobed; margins are entire (FIGURE 11). Venation is brochidodromous. Areolation is mostly well developed and is partially oriented. The simple or branched veinlets have moderately clavate endings which are not recurved. Veinlets consist of thin-walled, spirally thickened tracheary elements (probably tracheids) up to five times as wide as those found in the larger veins. Since the length of these enlarged elements remains constant, the resulting cells are roughly spherical. Thin-walled bundle sheath cells completely enclose the veinlets.

Surfaces of *Diclidanthera* leaves are nearly plane. Leaves are dorsiventral. Most species examined have a biseriate palisade layer with some triseriate regions. *Diclidanthera octandra* has a uniseriate palisade layer with some biseriate regions; *D. laurifolia* and *D. penduliflora* may have small uniseriate regions in an otherwise biseriate palisade. It is difficult to draw firm conclusions concerning the shape of the palisade cells because of the poor preservation of some of the material. In some of the species (*D. elliptica*, *D. laurifolia*, *D. octandra*, and *D. penduliflora*), the palisade cells appear very squat, sometimes almost square. I suspect that this is related to the manner in which leaves were pressed and dried, for one specimen of *D. penduliflora* displays typical, vertically elongated palisade cells. *Diclidanthera bolivarensis* also displays typical palisade cells, except for a few cells which are divided periclinally in the middle, yielding squat, almost square cells. The boundary between the palisade and spongy layers is often indistinct. Spongy mesophyll is of the typical lacunose type, with some compaction next to the abaxial epidermis. Spongy mesophyll cells having the same horizontal aspect noted in *Barnhartia* occur in *D. elliptica*, *D. laurifolia*, and *D. octandra*, but to a lesser degree. This feature may also be related to the pressing of leaves when they were prepared as herbarium specimens.

Rhomboid and polyhedral crystals are common in the bundle sheath cells of *Diclidanthera*. In addition, other crystalline forms occur in these cells in *D. bolivarensis* and *D. laurifolia*. The former species has very small, lenticular crystals, and two crystals sometimes intersect one another in some of the palisade cells. The latter species has groups of small druses in cells of the upper palisade and, to a lesser degree, in cells of the lowest portion of the spongy mesophyll.

All veins except the primary vein have a single collateral bundle. The primary vein is more complex and is dominated by a large arc of xylem on the abaxial side of the vein. This xylem arc is flanked by phloem on its abaxial side. In transverse section, a smaller area of xylem occurs on the adaxial side of the bundle. The smaller xylem area is flanked by phloem on its adaxial side. Between the two areas of xylem is a pithlike region of parenchyma, some of which breaks down to yield lacunae adjacent to the abaxial xylem. The terminal veinlets lack phloem.

The primary vein has a thick sheath of sclerenchyma between the vascular tissue and the bundle sheath. The smaller veins also have sclerenchyma sheaths. The width of the sheath decreases with decreasing vein size; the terminal veinlets lack sclerenchyma altogether.

A bundle sheath covers the entire vein system from primary vein to terminal veinlets. In larger veins, bundle sheath cells are thickened on their radial and inner tangential walls. Coincident with the decrease in the sclerenchyma sheath is a decrease in the thickening of the bundle sheath cells until, in the terminal veinlets, the bundle sheath cells have no secondary thickening at all. Bundle sheath extensions are absent.

The lower epidermis in *Diclidanthera* is uniseriate. The upper epidermis is triseriate over the primary vein and biseriate elsewhere, except in *D. bolivarensis*, where it is mostly triseriate with some biseriate patches. *Diclidanthera laurifolia* has some triseriate patches other than those over the primary vein.

In face view, leaf epidermal cells are polygonal. All species have pairs of cells in the epidermis which are similar to those in *Barnhartia* (FIGURE 13). In *D. bolivarensis*, *D. elliptica*, and *D. laurifolia* numerous epidermal cells are paired, whereas in *D. octandra* and *D. penduliflora* only a few paired cells occur.

In sectional view, epidermal cells are generally rectangular, although some square cells are seen. The cuticle is smooth-surfaced and varies in thickness from 1 to 4 μm.

Stomata are restricted to the lower epidermis, where they occur randomly over the surface. The stomatal apparatus is anomocytic (FIGURE 13). Guard cells are reniform; a pair nearly circular (length/width = 1.01). The guard cells have a prominent outer cuticular ridge which extends beyond the surface of the leaf, as well as an inconspicuous inner ridge. In median cross section, the guard cells have thickened periclinal walls and thin anticlinal walls.

Neither collection of *D. laurifolia* has trichomes; both collections of *D. penduliflora* have hairs, as do *D. elliptica* and *D. octandra*. Trichomes are heavily cuticularized and consist of uniseriate hairs divided into several cells by thin septa. Trichomes occur on both sides of the leaf and may be plentiful (*D. elliptica*) or very sparse (*D. octandra*).

No hydathodes were observed.

Eriandra fragrans

WOOD. Growth arcs are present (FIGURE 6). Pores are of uniform size distribution. The arrangement of pore groups is 89.6% solitary, 9.6% clusters, and 0.8% radial multiples. Radial multiples occur in only one of the four specimens studied (*Boschwezen 5810*). Pore outline is circular or slightly angular in some of the narrower vessels. Vessel wall thickness varies from 3.4 to 6.8 μm. Tangential pore diameter averages 180 μm., with a range of 41 to 330 μm. Perforation plates are exclusively simple, generally with round perforations which have only a very slight border

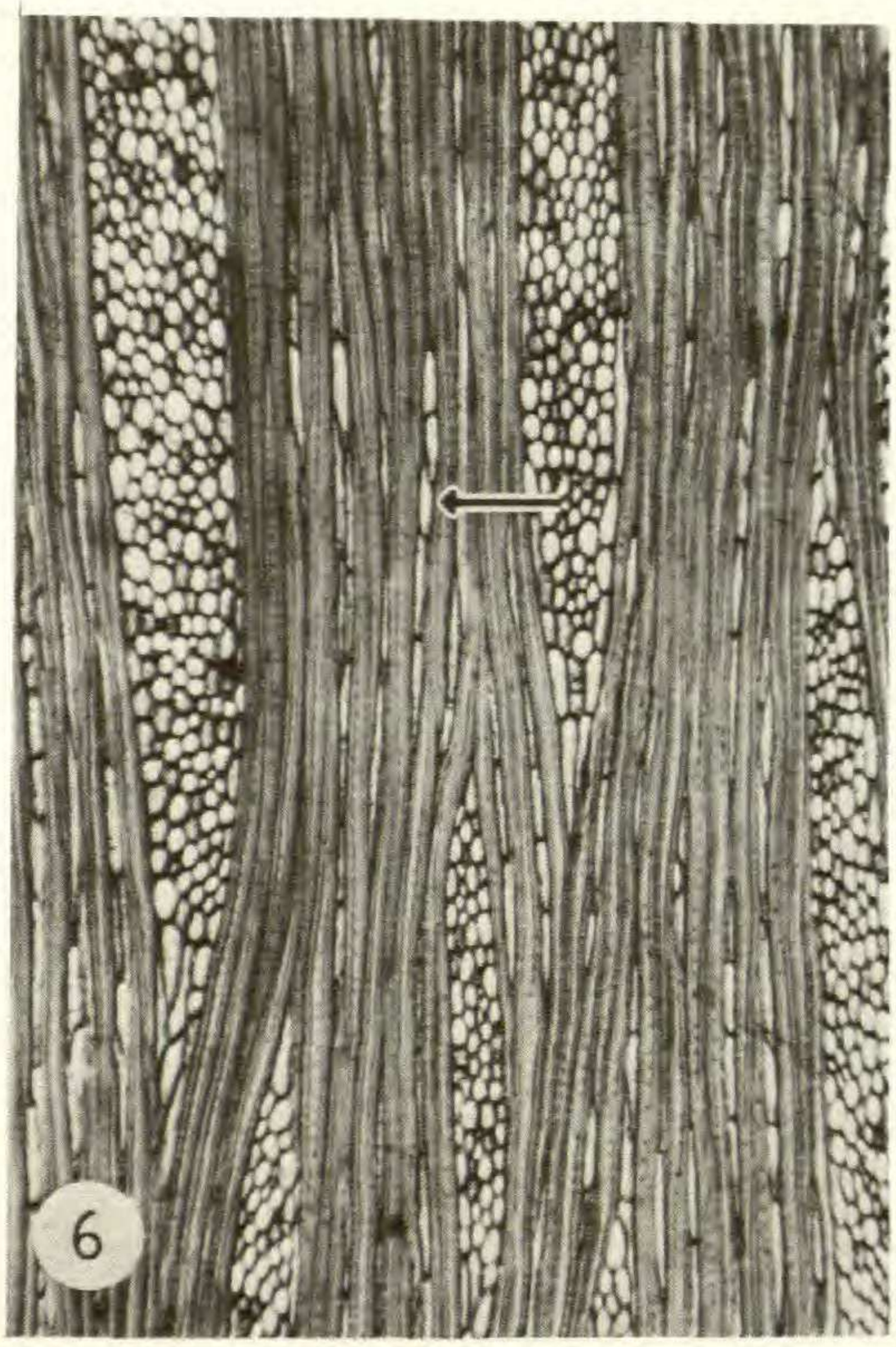
or no border at all. Tyloses are present in some of the specimens (FIGURE 8). In specimens having tyloses, the number varies from few to many per section, and the tyloses are usually abundant in those vessels where present. Both thin-walled and sclerotic tyloses may be present in the same wood. Vessel element length averages 780 μm., with a range of 55 to 1990 μm. Intervascular pitting is alternate; pits are usually oval- or circular-bordered, although there is some range in shape from elongate to nearly polygonal, the latter occurring where pits are crowded. Pit-border diameter ranges from 6.7 to 14 μm. Inner apertures are slitlike and crossed. Vessel element end wall angle ranges from 9° to 89°. Imperforate tracheary elements have a complete range of form from tracheids to distinct fiber-tracheids. The inner aperture does not extend beyond the edge of the border, as is common in fiber-tracheids of woods of many plants. The inner aperture is horizontal in the tracheids, vertical in the fiber-tracheids, and intermediate in position in transitional elements. Imperforate tracheary element wall thickness ranges from 3.4 to 11 μm., with the average length ranging from 340 to 2800 μm. (av. 1453 μm.).

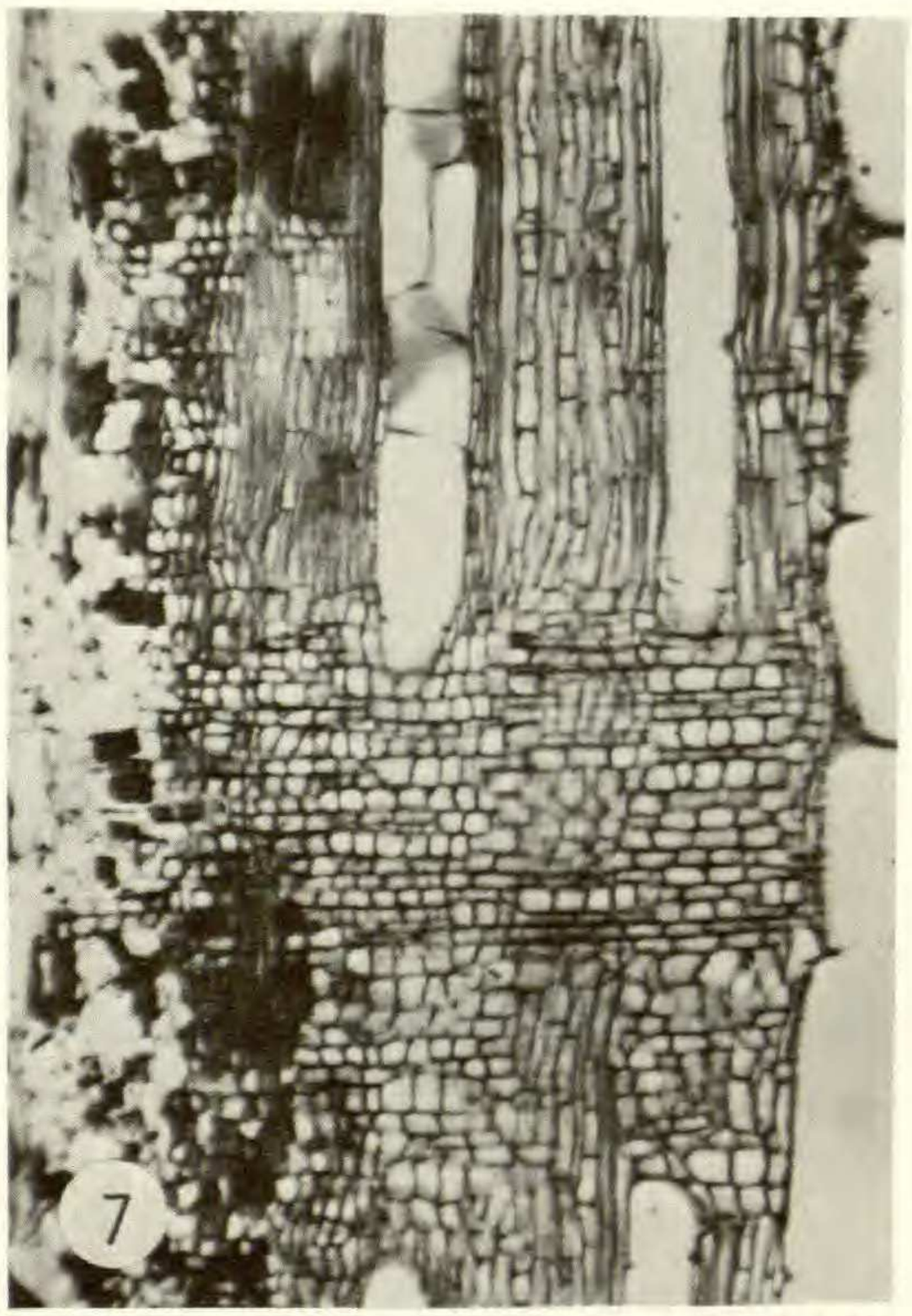
Vascular rays are both homocellular and heterocellular (FIGURES 6, 8). Homocellular rays are largely uniseriate; however, biseriate rays also occur. Homocellular rays vary in width from 14 to 37 μm., and are from 1 to 17 cells (140 to 1920 μm.) high. All cells are erect. Heterocellular rays are mostly multiseriate, but a few biseriate and uniseriate heterocellular rays occur. Ray width varies from 1 to 13 cells (20 to 370 μm.), and height from 6 to 130 cells (380 to 4740 μm.). The body of the heterocellular ray is composed of procumbent cells, with groups of square or short erect cells occurring throughout the ray (FIGURE 4). Uniseriate wings of 1 to 7 tall erect cells are usually present. These long uniseriate wings create some vertically fused rays. The nature of the ray is strongly influenced by the proximity of included phloem (FIGURE 5). The portion of a multiseriate ray produced immediately exterior to a patch of included phloem is much wider than that portion of the same ray at a greater distance from the phloem. For example, a xylem ray that is 10 cells wide next to the included phloem, narrows gradually with increasing radial distance from phloem until its width may be stabilized at only three cells.

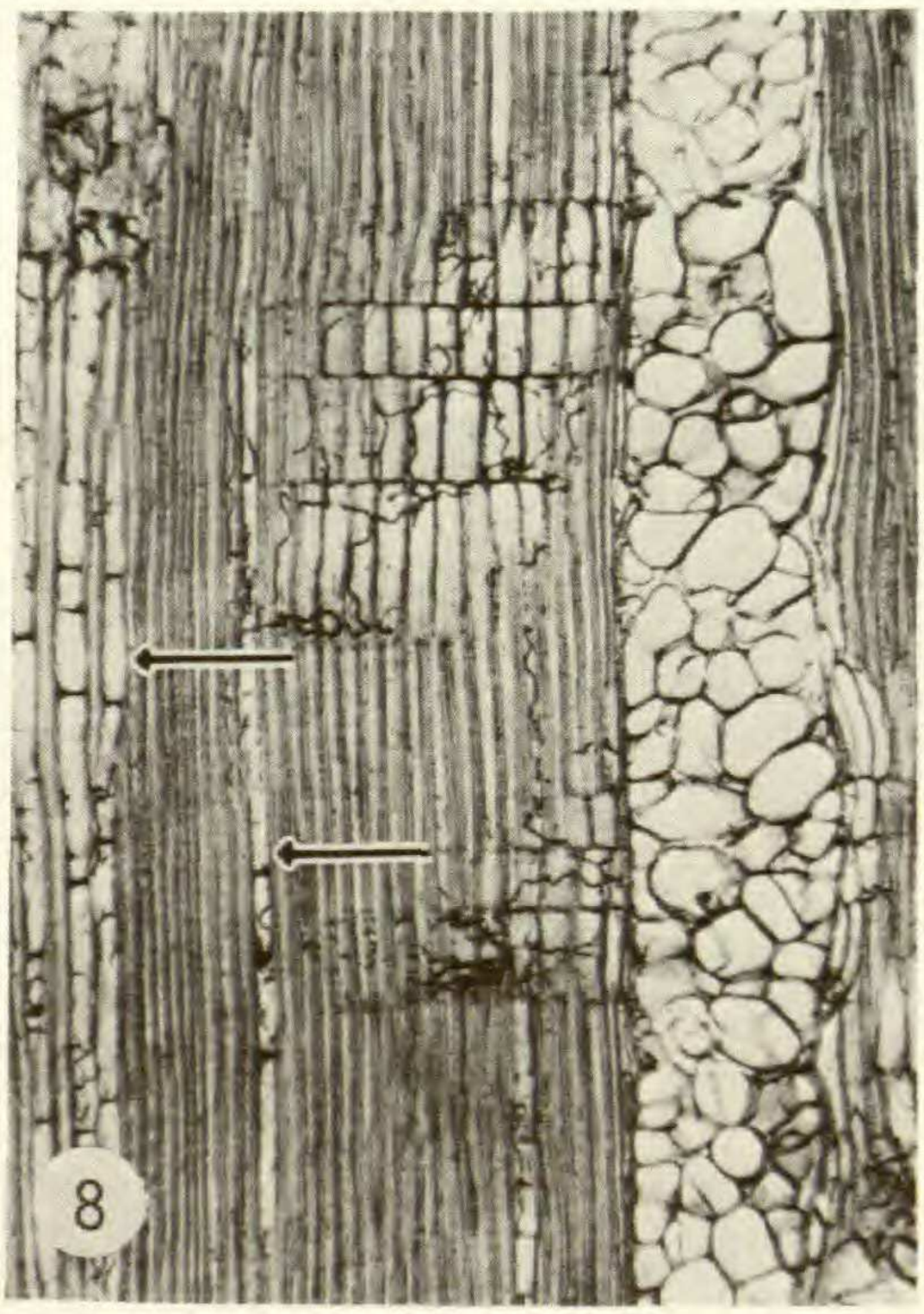
In three specimens, resumption of xylem production following a period of included phloem production was preceded by production of parenchyma which resembles the pith in organization. This loosely organized parenchyma ceases fairly abruptly with resumption of normal xylem production except where a ray arises in the xylem. When this happens, the loosely organized parenchyma extends somewhat into the xylem and, with increasing distance outward from the included phloem, it gradually becomes organized into a ray. The fourth specimen examined had little or no parenchyma of this kind produced between the included phloem and the normal xylem.

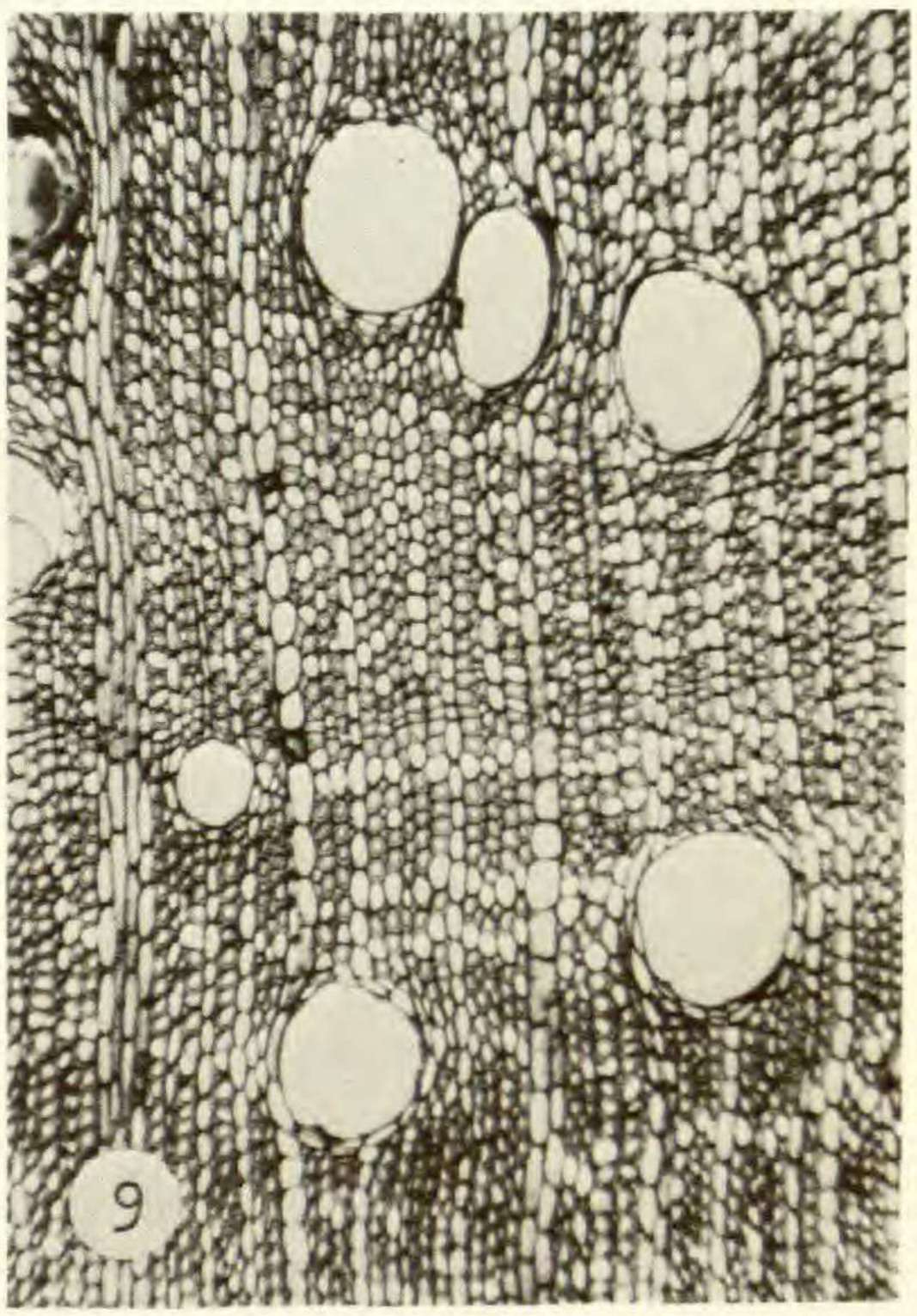
Vessel to ray parenchyma pitting is half-bordered. The ray side of the pit-pair usually has a simple pit corresponding to the border on the vessel side. Occasionally, the simple pit on the ray side of the pit-pair is

FIGURE 5: *Eriandra fragrans*, tangential section of stem showing included phloem (between arrows), × 12.









FIGURES 6–9: 6, *Eriandra fragrans*, tangential section of wood showing homocellular uniseriate rays (arrow) and heterocellular multiseriate rays with upright cells along margins and in wings, × 36; 7, *Moutabea longifolia*, radial section of stem showing included phloem (on left side) and a tall heterocellular ray, × 36; 8, *Eriandra fragrans*, radial section of wood showing vessel filled with tyloses, homocellular ray of erect cells, and axial xylem parenchyma (arrows) (note hyphae of fungus in ray), × 36; 9, *Eriandra fragrans*, transverse section of wood showing axial xylem parenchyma distribution (diffuse and tangential apotracheal and paratracheal diffuse with wings are visible), × 36.

larger than the pit on the vessel side. Sometimes the simple pit is large enough to encompass two pits on the vessel side, thus forming a unilaterally compound pit-pair. The vessel side of the pit-pair usually has a circular border and a slitlike inner aperture; sometimes, however, the inner aperture is enlarged to an oval shape.

Polygonal to rhomboid crystals occur in the rays of all specimens of *Eriandra*. Occasionally, in tangential section, erect cells were noted along the sides of the rays, but no real sheath was ever seen.

Axial xylem parenchyma is both apotracheal and paratracheal (FIGURE 9). Apotracheal parenchyma is mostly tangential, but some diffuse parenchyma also occurs. Paratracheal parenchyma is either aliform or paratracheal-diffuse with wings. In vessel to axial parenchyma pitting, the pit-pairs are half-bordered with a circular border and a slitlike inner aperture occurring on the vessel side.

INCLUDED PHLOEM. Included phloem is abundant and can be identified by the presence of sieve tube elements having compound sieve plates. Sclereids occur in the included phloem. Distribution of included phloem is shown in FIGURE 1.

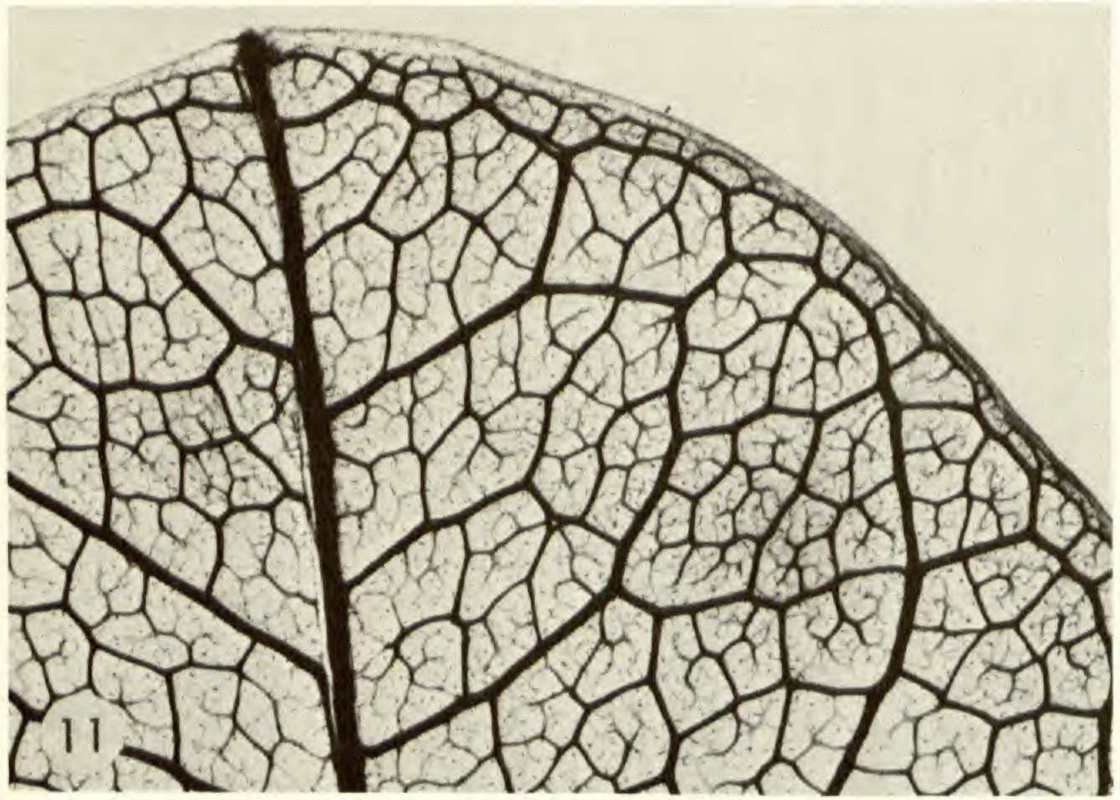
LEAVES. *Eriandra* leaves are simple and unlobed; margins are entire. Venation is brochidodromous. Areolation is mostly well developed and partially oriented. Veinlets are simple or branched, taper gradually to their ends, and are recurved. They consist of fibers with circular-bordered pits. Dense protoplasts are often concentrated at the distal ends of the fibers, but may be absent. Bundle sheath cells, thickened on their inner tangential and radial walls, entirely surround the veinlets.

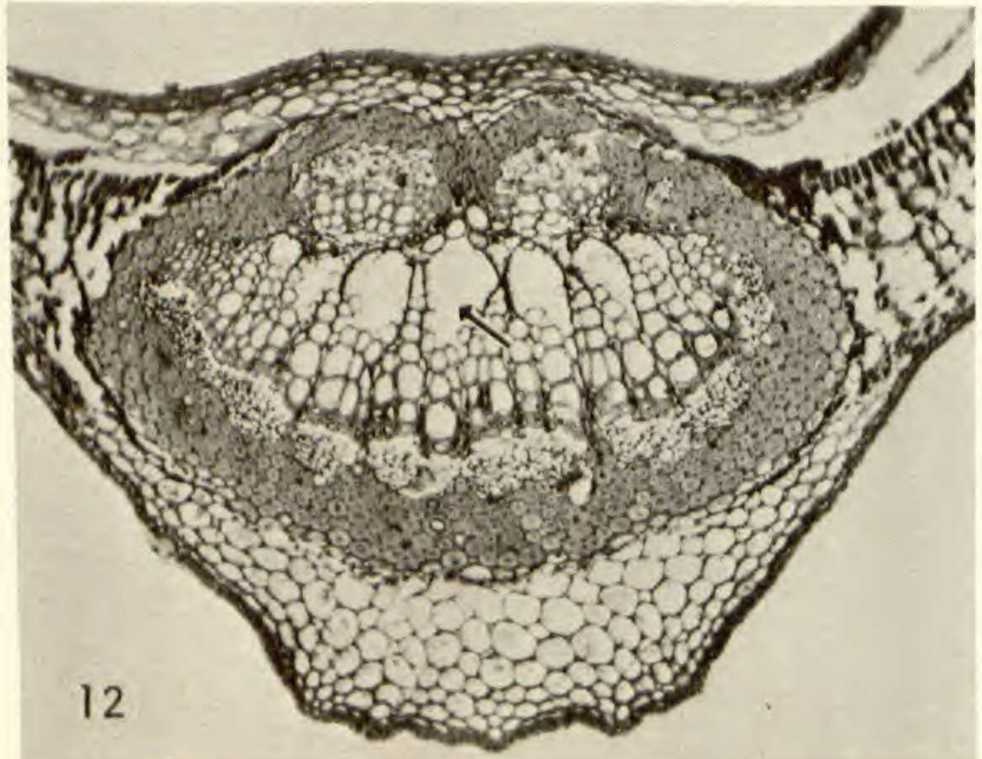
Surfaces of *Eriandra* leaves are flat and the leaves are dorsiventral. The palisade layer is uniseriate with some biseriate areas and is of typical configuration. The spongy layer is of the typical dicotyledonous type, except that some cells in the lower part of the layer have prominent secondary thickenings.

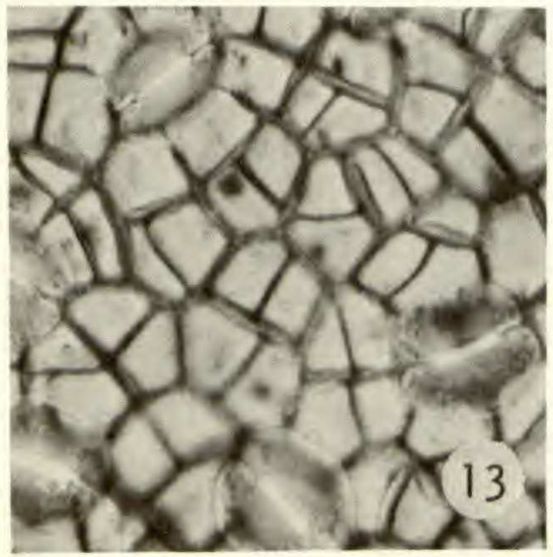
Rhomboid to polyhedral crystals are plentiful in bundle sheath cells and occur regularly in cells of the palisade layer. Similar crystals occasionally occur in cells of the pithlike central area of the primary vein.

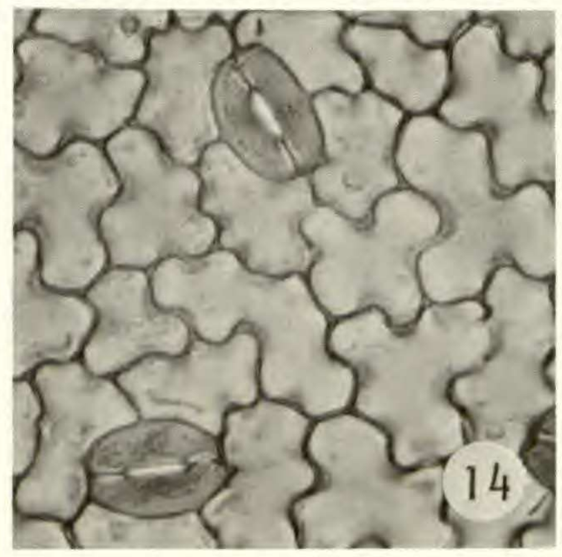
All veins except the primary vein have a single collateral bundle. The primary vein (as seen in transverse section) has a large area of xylem with one long band (or several shorter bands) of phloem adjacent to it on the abaxial side. Adaxial to this large area of xylem and phloem, and separated from it by an area of parenchyma, are one to several smaller xylem areas with phloem flanking each of them on their adaxial sides. Vascular tissue of the primary vein is surrounded by a thin sheath of sclerenchyma. Sometimes a large lacuna is visible in the center of the primary vein. Terminal veinlets lack xylem and phloem.

All veins are ensheathed in fibers that have circular-bordered pits. Although these fibers cannot be classed as either xylem or phloem, they appear to have differentiated from procambium. As the size of the vein









FIGURES 10–14: 10, *Moutabea* sp. (*Wurdack & Adderly 43409*), isolated sclereids from leaf, × 90; 11, *Diclidanthera elliptica*, leaf clearing showing brochidodromous venation, × 6; 12, *Barnhartia floribunda*, transverse section of leaf primary vein showing lacunae (arrow), × 85; 13, *Diclidanthera bolivarensis*, paradermal section of leaf through abaxial epidermis, × 515; 14, *Eriandra fragrans*, paradermal section of leaf through abaxial epidermis, × 375.

decreases, the amount of xylem and phloem decreases until first the phloem is no longer present and then, in the ultimate veinlets, the xylem is also absent, leaving only the fiber sheath surrounded by the bundle sheath. Bundle sheath cells are thickened on their radial and inner tangential walls and ensheath all vein sizes. Bundle sheath extensions are absent.

The lower epidermis is uniseriate; the upper epidermis is either uniseriate or biseriate.

In face view, epidermal cells of both leaf surfaces are sinuous (FIGURE 14). The amount of waviness varies according to the specimen, from slightly to moderately wavy. The outer layer of the adaxial epidermis differs from the inner layer in two ways: the inner layer has larger cells, and the anticlinal walls of its cells are straight or are less sinuous than those of the outer layer.

In sectional view, epidermal cells are square to rectangular. The cuticle is smooth-surfaced, varying in thickness from 1.4 to 2.7 μm.

Stomata are restricted to the lower epidermis and are evenly distributed over its surface. The stomatal apparatus is anomocytic (FIGURE 14). Guard cells are reniform; a pair elliptical (length/width = 1.32). They are provided with a prominent outer cuticular ridge which projects from the guard cell over the stoma, parallel with the surface of the leaf. An inconspicuous inner ridge is also present. A cross section through the guard cells reveals thin anticlinal walls and thickened periclinal walls.

No trichomes or hydathodes were observed.

Moutabea

WOOD. Faint growth arcs occur; pores are of uniform size distribution. Pore distribution is mostly solitary (80–92%, average for all species 85%) with a substantial fraction of pore clusters (8–18%, average for all species 14%) and a few radial pore multiples (0–3%, average for all species 1.4%). One very young portion of the wood of *Moutabea* sp. (*Wurdack & Adderly 43409*) has 91% solitary and 9% radial pore multiples. Pore outline is circular to somewhat angular in the smaller vessels. Vessel wall thickness varies from 3.4 to 9.5 μm. Tangential pore diameter averages 180 μm. with a range of 34 to 360 μm. Perforation plates are simple; borders are absent or vestigial on the round perforations. Tyloses are present and vary from thin-walled to thick-walled. The lumina of the tyloses may be nearly occluded in those having the thickest walls. The number of tyloses varies from few to many per section and from few to many per vessel. Vessel element length averages 620 μm., with a range of 110 to 1440 μm. Variation in length within a species is as great as that between species. For example, average vessel element lengths for three specimens of *M. guianensis* are 550 μm., 580 μm., and 750 μm.; for the single specimens of *M. longifolia* and *Moutabea* sp. (*Wurdack & Adderly 43409*), 610 μm. and 540 μm., respectively. Intervascular pitting is alternate; pit borders are circular to oval, sometimes grading to polygonal. The diameter

of the pit border ranges from 7.4 to 12 μm. Inner apertures are slitlike and only slightly crossed. Vessel element end wall angle ranges from 1° to 89°. Imperforate tracheary elements vary from tracheids to fiber-tracheids. Pits of the imperforate tracheary elements are circular-bordered with slitlike apertures; wall thickness varies from 2.7 to 9.5 μm.; cell length varies from 340 to 1440 μm. (av. 890 μm.).

Vascular rays are both homocellular and heterocellular. Homocellular rays are nearly all uniseriate, ranging from 7 μm. wide in the uniseriate rays to 29 μm. in some of the biseriate rays. Biseriate rays usually have extensive uniseriate wings. Height of homocellular rays varies from 1 to 15 cells (51 to 1130 μm.). Heterocellular rays are mostly biseriate or multiseriate, but may vary in width from 1 to 16 cells (10 to 410 μm.). Height varies from 3 to 138 cells (140 to 5640 μm.). Vertically fused rays are common, as are uniseriate wings. Cells of heterocellular rays range from procumbent to square to upright (FIGURE 7); uniseriate wings are formed of upright cells.

Proximity of xylem rays to included phloem influences their structure as follows: immediately external to included phloem, the xylem consists of areas of homogeneous, pithlike parenchyma; with increasing radial distance from the included phloem, this xylem parenchyma gradually becomes organized into indistinct rays by the intercalation of imperforate tracheary elements among the parenchyma cells; finally, it is organized into the distinct rays characteristic of typical xylem.

Vessel to ray parenchyma pitting is half-bordered; the vessel side of the pit-pair has a circular border and a slitlike inner aperture, the ray side a simple pit corresponding to the border on the vessel side. Inner apertures of closely adjacent pit-pairs are often fused into one large aperture. Rhomboid to polyhedral crystals occur in rays of *M. guianensis* and *Moutabea* sp. (*Wurdack & Adderly 43409*) but are not present in *M. longifolia*. The fluid-preserved specimen of *M. guianensis* contains several types of deposits in ray cells: some cells have a large sphere, others many small spheres, and others granular masses. The chemical composition of these deposits is not known. Spherical starch grains were identified using polarized light. Some upright cells occur on the periphery of the ray, but no definite sheath of cells is present.

Both apotracheal and paratracheal axial xylem parenchyma are present. Apotracheal parenchyma is diffuse or tangential. Paratracheal parenchyma is mostly diffuse with wings, although a little aliform parenchyma is present. In *M. guianensis* aliform parenchyma is the major type of axial xylem parenchyma encountered in immature wood produced prior to the first included phloem. Crystals do not occur in the axial parenchyma; starch grains were seen in fluid-preserved wood. Vessel to axial parenchyma pitting is half-bordered, with the border occurring on the vessel side of the pit-pair.

INCLUDED PHLOEM. Included phloem is distributed in crescent-shaped, more or less concentric segments and may be identified by the presence of

sieve tube elements with compound sieve plates. Fibers and sclereids also occur.

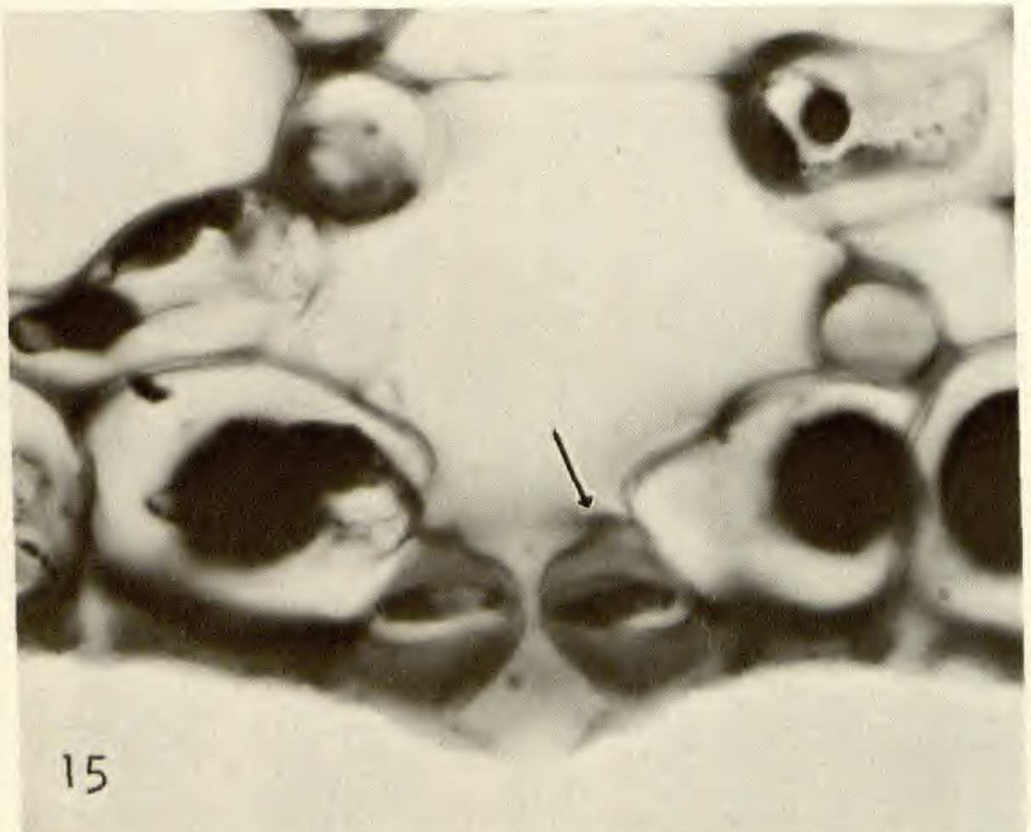
LEAVES. *Moutabea* leaves are simple and unlobed; margins are entire. Venation is brochidodromous. Areolation is mostly well developed and partially oriented. Veinlets are simple or branched, have clavate endings, and are not recurved. They consist of large, thin-walled, expanded, spirally thickened tracheary elements (probably tracheids). The last element in the veinlet is often expanded greatly, sometimes being almost spherical; it is usually associated with a columnar sclereid (FIGURE 16). Unthickened bundle sheath cells entirely encase the veinlets.

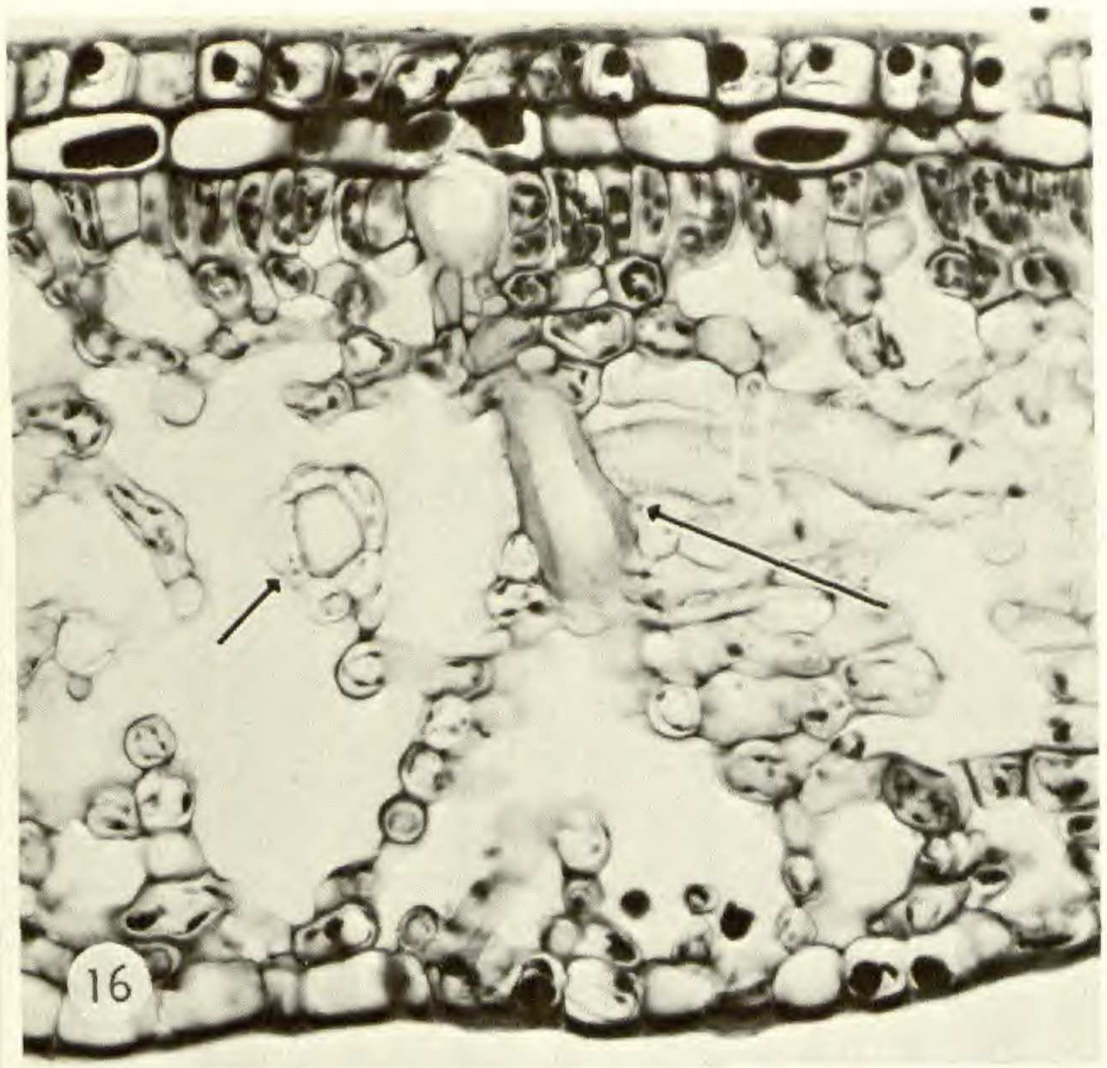
Surfaces of *Moutabea* leaves are flat. Leaves are dorsiventral. The palisade layer is usually uniseriate or biseriate. However, *Moutabea* sp. (*Wurdack & Adderly 43409*) has a third layer transitional between palisade and spongy layers; *M. excoriata* is triseriate; one specimen of *M. guianensis* (*Van Donselaar 3193*) is multiseriate, having from four to five tiers of cells in the palisade layer. The spongy layer is the usual lacunose type.

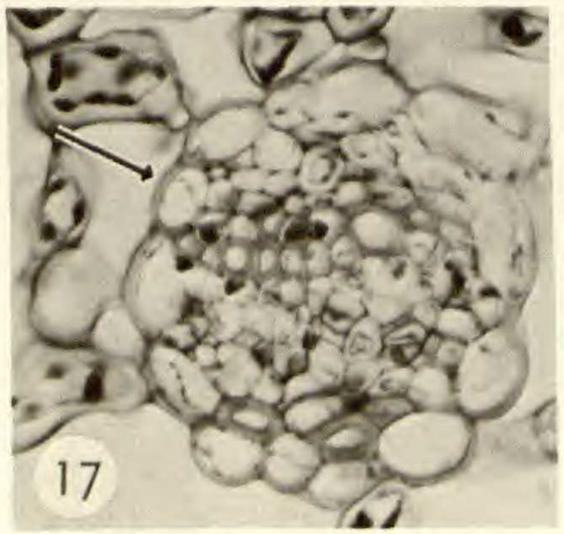
Rhomboid and polyhedral crystals occur in *M. aculeata*, *M. excoriata*, and *M. guianensis*, but not in *M. longifolia*. These crystals occur in bundle sheath cells of *M. aculeata* and *M. guianensis*. Some of the species have similar crystals in cells of the palisade and spongy layers. Druses occur in idioblasts in the palisade layer of *Moutabea* sp. (*Wurdack & Adderly 43409*). Spherical aggregations of small anisotropic particles embedded in dark, isotropic, amorphous masses occur in cells of the spongy layer of *M. longifolia* and in cells of the lower epidermis of *M. guianensis*. The insolubility of this material in dilute HCl indicates that it is neither calcium oxalate nor calcium carbonate, two crystalline substances commonly found in plant cells.

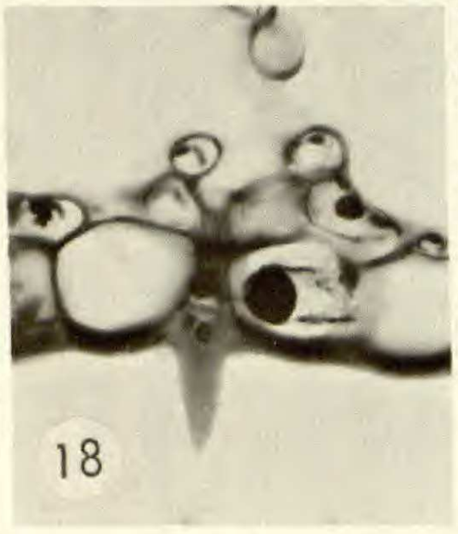
Vascular bundles vary in construction with size. The primary vein differs slightly among species. Basically, as seen in transverse section, it consists of a large area of xylem flanked by phloem in the normal abaxial position. In addition, there are one or sometimes two or three smaller areas of xylem flanked by adaxial phloem over the main vascular supply noted above. Parenchyma extending laterally from one side of the vascular bundle to the other creates a central pithlike region. All of this is surrounded by one to three layers of sclerenchyma cells. In *Pulle 389* (*M. guianensis*), xylem areas are joined, and are surrounded by phloem, to form a ring of xylem surrounded by a ring of phloem with parenchyma in the middle. Medium-sized veins consist of a collateral bundle surrounded by a bundle sheath whose cells are thickened on the outer tangential and radial walls (FIGURE 17). The smallest veins lack phloem, and the bundle sheath cells are not usually thickened. Bundle sheath extensions are absent.

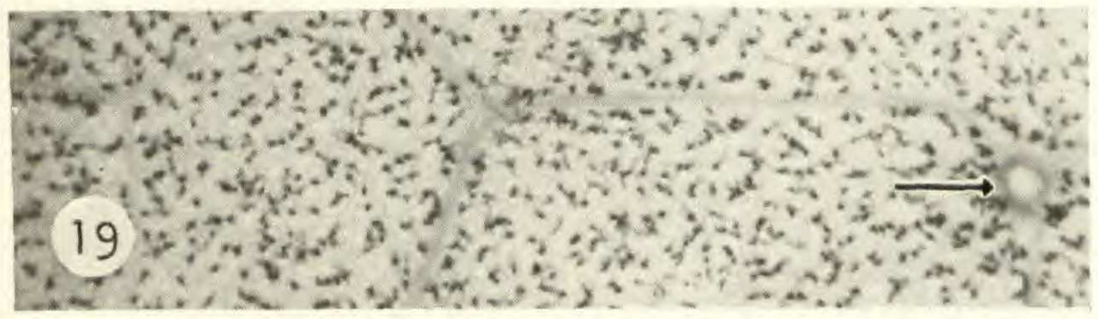
The lower epidermis is uniseriate. The upper epidermis is three to four layers thick over the primary vein, tapering quickly to one or two layers over the rest of the blade. Two specimens of *Moutabea guianensis* have











FIGURES 15–19: 15, *Moutabea guianensis*, leaf transverse section through abaxial epidermis showing median cross section of stomatal apparatus (note inner ledge on guard cell (arrow)), × 1050; 16, *Moutabea guianensis*, transverse section of leaf showing terminal position of sclereid (long arrow) and bundle sheath around terminal veinlet (short arrow), × 240; 17, *Moutabea guianensis*, transverse section of leaf showing cross section of medium-sized vein (note unevenly thickened bundle sheath cells (arrow)), × 360; 18, *Moutabea guianensis*, transverse section of leaf showing hair on abaxial epidermis, × 360; 19, *Moutabea guianensis*, leaf clearing showing distribution of sclereids (black dots) (note nectary on abaxial surface (arrow)), × 13.

a uniseriate upper epidermis; a third specimen has a biseriate epidermis. Thus, the number of epidermal layers cannot have much importance in distinguishing species.

In face view, the epidermal cells of both leaf surfaces are polygonal. In *M. guianensis* and *M. longifolia*, cells of the second epidermal layer are noticeably larger than those of the outer layer. The epidermal cells of *M. excoriata* and *Moutabea* sp. (*Wurdack & Adderly 43409*) are approximately the same size in both layers. The *Wurdack & Adderly* specimen is unique among the moutabeas studied, in possessing paired epidermal cells similar to those described in *Barnhartia*. These paired cells differ from those in *Barnhartia*, however, because they occur in the inner instead of the outer epidermal layer.

In sectional view, epidermal cells are square to rectangular. Often cells of the outer layer of the upper epidermis are elongated perpendicularly to the plane of the leaf. Cuticle thickness usually varies from 1.4 to 4.1 μm. and is occasionally as thick as 5.4 μm.

Stomata are restricted to the lower epidermis and are evenly distributed. The stomatal apparatus is anomocytic. Guard cells are reniform; a pair is roughly circular (length/width = 0.97). The guard cells possess a prominent outer cuticular ridge which usually extends parallel with the plane of the leaf or sometimes projects slightly above the leaf surface. A less prominent inner ridge is also present (FIGURE 15). In median transverse section, guard cells have heavily thickened periclinal walls and thin anticlinal walls.

Trichomes are present in small numbers on the lower epidermis of *M. guianensis* (FIGURE 18) and in very small numbers (2 trichomes in 54 transverse sections) on the lower epidermis of *M. excoriata*. Trichomes are similar in both species and consist of outgrowths of epidermal cells. They extend above the leaf surface to a height about equal to the thickness of a normal epidermal cell. No trichomes were observed in the other species of *Moutabea*.

No hydathodes were observed.

All species of *Moutabea* possess columnar sclereids in the leaves. Sclereids are variously thickened; often the lumen is nearly occluded. Walls consist of many concentric lamellations easily visible both with and without polarized light. Generally, the adaxial end of a sclereid is truncated, while the abaxial end tapers to a point (FIGURE 10). Sclereids of different species show various degrees of branching and various densities within the leaf (FIGURE 19). The adaxial ends of the sclereids usually terminate just inside the inner layer of the upper epidermis. Where more than one epidermal layer is present, some small branches of the sclereid usually penetrate to the inner side of the external layer of epidermal cells. The abaxial ends of the sclereids usually terminate in the spongy layer close to the lower epidermis. Sclereids are regularly associated with terminal veinlets and may therefore be called "terminal sclereids" (FIGURE 16).

DISCUSSION AND CONCLUSIONS

Wood Anatomy of Moutabeae

Woods of the Moutabeae are very homogeneous and no clear differences in xylem that might be used to separate the genera can be distinguished. This fact is clear even though two of the genera studied are represented by very immature material. Several xylem characteristics are common to the tribe. Growth arcs are present in all material except the immature specimens of *Diclidanthera penduliflora* and *Barnhartia*. Pores are uniformly distributed and overwhelmingly solitary (80–90%), but clusters also occur in all genera except in the immature specimens of *Barnhartia*. In the wood of *Moutabea* sp. (*Wurdack & Adderly 43409*), for example, pore clusters do not appear until after the first segments of included phloem are produced. Pores are generally round to slightly angular in some of the narrower vessels. Pore diameter shows no significant differences among genera that can not be attributed to age variations in the wood samples (Cumbie, 1960). For example, in *Moutabea* sp. (*Wurdack & Adderly 43409*), average pore diameter is 62 μm. inside the first-formed included phloem and 120 μm. in later-formed wood. Average pore diameters in young wood of *Barnhartia* and *Diclidanthera* (48 μm. and 46 μm., respectively) are similar to average pore diameters interior to the first-formed included phloem in *Moutabea* sp. (*Wurdack & Adderly 43409*). While average pore diameters for *Moutabea* (180 μm. and *Eriandra* (180 μm.) as a whole are higher than for *Moutabea* sp. (*Wurdack & Adderly 43409*), I do not believe this is significant, especially in light of total variation in pore size of mature wood (e.g., 34 to 360 μm. in *Moutabea*).

Perforation plates are exclusively simple with round perforations. That tyloses occur in *Eriandra* and *Moutabea* and are absent in *Diclidanthera* and *Barnhartia* is most likely another reflection of variation with age. Differences in vessel element length can be attributed to sample habit (tree, vine, shrub), sample source (location in the plant), and sampling error (Bailey & Tupper, 1918; Carlquist, 1961). The same may be said of pit diameter, vessel element end wall angle, and imperforate tracheary element length.

Intervascular pitting is alternate; pits are usually circular-bordered but may become polygonal when closely spaced. Imperforate tracheary elements range from tracheids to fiber-tracheids. Vascular rays may be homocellular or heterocellular. Homocellular rays are mostly uniseriate, occasionally biseriate, and vary in height from 1 to 15 cells. Heterocellular rays are uniseriate to multiseriate, occasionally up to 16 cells in width, may surpass 100 cells in height, and commonly have long uniseriate wings. Again, structural differences among genera may be attributed to variables of sample source, age, and species habit (Carlquist, 1961). Diffuse and tangential apotracheal, and diffuse paratracheal with wings are the main types of axial xylem parenchyma. Arcs or partial rings of

included phloem are present in all genera except *Barnhartia*. I strongly suspect older wood of *Barnhartia* would also display included phloem since overall growth and appearance of *Barnhartia* closely resembles that of other woody climbers in the family (Sprague & Sandwith, 1932).

The term "conjunctive tissue" has been used to refer to parenchyma associated with included phloem (Chalk & Chattaway, 1937; Eames & MacDaniels, 1947; Committee on Nomenclature, 1957; Fahn, 1974), and does not indicate whether such tissue had its origin in xylem or phloem. Since "conjunctive" parenchyma in Moutabeae is clearly xylem parenchyma, use of the term "xylem parenchyma" is preferable: it is more informative than the noncommittal term "conjunctive" parenchyma and it is not liable to misinterpretation.

The types of axial parenchyma present in Moutabeae are difficult to identify and place into established categories. This is because of the irregular configuration of the wood caused by the included phloem. Consequently, anatomists have not been consistent in their descriptions of axial xylem parenchyma in Moutabeae. Metcalfe and Chalk (1950) state that *Moutabea* has predominantly diffuse or banded apotracheal parenchyma, Biswas (1969) reports diffuse-in-aggregates apotracheal and scanty paratracheal, and Record and Hess (1943) report metatracheal (banded apotracheal) and vasicentric paratracheal. Comparison of these descriptions with mine (diffuse and tangential apotracheal, paratracheal diffuse with wings, and a small amount of aliform paratracheal parenchyma) shows that most of the inconsistencies arise either from different terminologies used by other botanists or from their failure to include one or more types of parenchyma in their description. The outstanding differences between my descriptions and those of other botanists is my report of wings associated with the diffuse paratracheal parenchyma and of the presence of aliform parenchyma.

Hegnauer (1969) has noted in several families (e.g., Iridaceae, Gramineae, Labiatae) that tropical members store starch while temperate members store carbohydrates other than starch. Since he found copious amounts of starch in *Securidaca*, a tropical member of the Polygalaceae, and none in a number of temperate members, he suggests that a parallel situation may exist in the Polygalaceae. According to Hegnauer's hypothesis, all members of the Moutabeae should store starch. However, starch was observed in only one specimen, the sole fluid-preserved specimen.

LEAF ANATOMY OF THE MOUTABEAE

Although the leaves of the Moutabeae show greater structural variation than the xylem, there is, nevertheless, a basic leaf structure characteristic of the tribe. Leaves are simple and unlobed with entire margins. Venation is brochidodromous; areolation is mostly well developed and partially oriented. Veinlets are simple or branched and encased in bundle sheaths. Bundle sheath extensions are absent. No hydathodes are present.

Surfaces of the leaves are flat with no pronounced topographic features.

Leaves are dorsiventral. A palisade layer 1 to 3 cells high and a well-developed lacunose spongy layer are present. Rhomboid to polyhedral crystals occur in bundle sheath cells of some species in all genera. All veins except primary veins have single collateral bundles. Veinlets lack phloem. Primary veins are large and appear to be constructed of a large collateral bundle which is separated from one or more smaller, inverted adaxial bundles by varying amounts of parenchyma.

The lower epidermis is uniseriate. The upper epidermis has biseriate regions in all species; in some species it may be triseriate.

Stomata are restricted to the lower epidermis. The stomatal apparatus is anomocytic. Guard cells are reniform and possess a prominent outer cuticular ridge; they have thickened periclinal walls and thin anticlinal walls.

There is a distinct difference between *Eriandra* leaves and those of the other three genera. In *Eriandra* leaves, vein endings taper, are recurved, and consist of fibers with bordered pits in the walls; epidermal cells are sinuous in outline and do not occur in pairs; guard cell pairs are elliptical (length/width ratio 1.3); and some parenchyma cells of the spongy mesophyll have prominent secondary thickenings. On the other hand, in *Barnhartia*, *Diclidanthera*, and *Moutabea* leaves, vein endings are clavate, straight, and composed of enlarged, spirally thickened tracheary elements; epidermal cells are polygonal in outline; paired epidermal cells occur in all species of *Barnhartia* and *Diclidanthera*, and in *Moutabea* sp. (*Wurdack & Adderly* 43409); guard cell pairs are round (length/width ratio 0.97–1.01); and parenchyma cells of the spongy mesophyll lack prominent secondary thickenings. Van Royen and van Steenis (1952) report a distribution for extrafloral nectaries which supports the separation of *Eriandra* from the other three genera: absent in *Eriandra*; present in *Barnhartia*, *Diclidanthera*, and *Moutabea*. Although I have not made a thorough study, I have observed extrafloral nectaries in *Barnhartia* at the distal end of the petiole, in *Diclidanthera* at the base of the blade, and in *Moutabea* on either side of the stem where the petiole is attached, as well as on the abaxial leaf surface.

While *Barnhartia*, *Diclidanthera*, and *Moutabea* form a group distinct from *Eriandra*, the group is not entirely homogeneous. For example, leaves of all species of *Moutabea* contain numerous columnar sclereids; similar sclereids are absent in *Barnhartia* and *Diclidanthera* (as well as in *Eriandra*). *Moutabea* differs from *Barnhartia* and *Diclidanthera* in two additional ways: first, while all species of *Barnhartia* and *Diclidanthera* have paired cells in the outer epidermal layer of the leaf, only one species of *Moutabea* (*Moutabea* sp. (*Wurdack & Adderly 43409*)) has paired epidermal cells, and these only occur in the inner epidermal layer; second, in *Moutabea*, bundle sheath cells are thickened on their outer periclinal walls, while in the other genera of Moutabeae, bundle sheath cells are thickened on the inner periclinal walls. *Barnhartia* and *Diclidanthera* leaves are too similar to separate anatomically.

Anatomy is seldom useful in separating species (Metcalfe & Chalk,

1950; Bailey, 1953), as is generally true here. However, the columnar sclereids of *Moutabea* offer a possible means of species discrimination (Foster, 1946, 1947; Rao, 1951, 1957). Foster's (1946) study of *Mouriria* Aublet (Melastomataceae) shows the extent to which sclereids can vary in a genus, and how this variation can be used to group species. However, Foster's study of foliar sclereids in *Trochodendron aralioides* Sieb. & Zucc., which reveals the ". . . remarkable fluctuation in the form and structure of such cells which can occur within a single species" (Foster, 1946), indicates that sclereids may not necessarily be useful taxonomically. While sclereids in different specimens of *Moutabea* differ slightly in branching and concentration, no consistent patterns could be detected.

Evolutionary Trends and Phylogenetic Relationships

According to Carlquist (1961) and others, vessel element specialization is the most reliable guide to evolutionary trends in the xylem. Primitive woods are those whose vessel elements most resemble tracheids (i.e., long, narrow, scalariformly pitted cells with scalariform perforation plates and angular transverse sections). Advanced woods are those whose vessel elements are short, broad, alternately pitted cells with simple perforation plates and round transverse sections. Many other features of xylem have been ranked as primitive or advanced by correlation with the degree of vessel element specialization (e.g., solitary pores, long imperforate tracheary elements, and lack of libriform wood fibers are considered primitive). Based on the following characteristics of *Eriandra* and *Moutabea* wood (these being the only genera for which mature wood was available), the Moutabeae appear to be intermediate, neither primitive nor very advanced. Vessel element length averages ca. 700 μm., which is very near the 649 μm. average found for 600 dicotyledons (Metcalfe & Chalk, 1950). Pore diameters average 180 μm., as compared to 94 μm. for 1500 dicotyledons (Metcalfe & Chalk, 1950). Pores are mainly solitary (87%; 12% occur in small clusters) and are round in outline. Intervascular pitting is alternate; perforations are simple. Imperforate tracheary elements, which consist of tracheids and fiber-tracheids, average 1170 μm. in length, as compared to 1317 μm. for 534 dicotyledons (Metcalfe & Chalk, 1950).

Acceptance of the evolutionary state of advancement indicated by these facts should be tempered by the realization that phylogenetic relationships may be masked by specializations related to a specific habit. This is effectively demonstrated by comparison of my study of Moutabeae with the Ayensu and Stern (1964) study of Passifloraceae. By comparing arboreal and lianous members of this family, they demonstrated that the following characters are correlated with the lianous habit: anomalous growth; short vessel elements; broad, solitary vessels; perforated fiber-tracheids; and absence of libriform wood fibers. This is remarkably similar to the situation in Polygalaceae tribe Moutabeae, which has short, broad vessel elements, and solitary vessels. While there are no perforated fiber-tracheids in the Moutabeae, there are long, narrow vessel elements

with very oblique end walls which might be described as "perforated tracheids" and which appear similar to the perforated fiber-tracheids of the Passifloraceae.

Significantly, *Eriandra*, whose wood shows all the lianous characters above, is a tree up to 25 meters tall and nearly a meter in diameter. The possession of anatomical traits normally associated with lianas might suggest they are structural relicts indicative of a lianous ancestry and might provide independent evidence that *Eriandra* is related to the other lianous members of the Moutabeae. Arboreal habit and somewhat longer, more specialized imperforate tracheary elements could indicate that *Eriandra* is diverging from the rest of the Moutabeae. Evidence from the leaves, which has been previously noted, strengthens the contention that *Eriandra* is becoming separated from the other genera of the tribe. That *Eriandra* should have diverged is not surprising considering its geographical separation from the other genera. This divergence can only be tentatively suggested since the changes noted are slight and might be associated with other variables such as habit or sampling.

No major evolutionary trends similar to those developed for secondary xylem have been developed for leaves. Perhaps this is because leaves vary so readily in response to habitat. However, because leaves seem to evolve faster than wood, they are often useful for studying evolutionary trends within families or genera (Carlquist, 1961; Tucker, 1964). On the morphological level, Hickey's (1973) study of leaf architecture promises to provide botanists with another means of studying plant phylogeny and evolution. He has found most dicotyledonous taxa to possess consistent patterns of leaf architecture. Although I have not made a detailed analysis of leaf architecture in Moutabeae, all genera appear alike superficially in that they have simple, entire leaves with brochidodromous venation.

Several anatomical features of leaves have been used as indicators of genetic relationships. As mentioned earlier, Moutabeae have similar mesophyll structure, crystals, bundle sheaths, vascular bundles (including primary veins), epidermal structure, and stomatal apparatus, all of which indicate that these genera might have had a common origin. There are also smaller differences, probably the result of evolution within the tribe, which allow the separation of *Eriandra* from *Barnhartia*, *Diclidanthera*, and *Moutabea*, and the separation of *Moutabea* from *Barnhartia* and *Diclidanthera*. *Eriandra* displays the greatest number of differences; *Moutabea* differs from the other genera in its columnar foliar sclereids.

Separation of *Eriandra* from the rest of the tribe is strengthened by study of the evolutionary origin of terminal columnar sclereids. Cells which occur at the terminus of a veinlet are referred to as "terminal" cells, e.g., terminal sclereids (Foster, 1946, 1947, 1956; Tucker, 1964). Foster (1946) first noted the restriction of sclereids to the ends of veinlets in his study of *Mouriria*. Terminal cells may either be normal conductive cells or idioblasts, the latter being referred to as "terminal idioblasts" (Tucker, 1964). If these idioblasts resemble tracheids in having spirally thickened or pitted walls, but differ from typical tracheids in form, size,

or general topography, they are termed "tracheoid idioblasts" (Foster, 1956). Tucker (1964) suggests that terminal cells show phylogenetic trends of specialization analogous with the evolutionary development of vessel elements and imperforate tracheary cells. Terminal sclerenchymatous idioblasts and terminal tracheoid idioblasts are believed to represent cell types which have evolved from normal conductive terminal vascular cells. Although ontogenetic studies such as those of Foster (1944, 1945) would be necessary to prove the procambial origin of sclerenchymatous idioblasts in Moutabeae, my own observations and those of Foster (1947) on the terminal nature of these cells argue strongly for their procambial origin. I have refrained from using the term "tracheoid idioblast" and have instead referred to such cells as "enlarged, spirally thickened tracheary elements." I have done this because I believe that the morphology and distribution of these cells does not warrant calling them idioblasts, and because they definitely look like tracheary elements and are not merely tracheoid. The presence of enlarged terminal tracheary cells in *Barnhartia*, *Diclidanthera*, and *Moutabea* indicates a tendency for change in the terminal cells of veins in these genera, providing additional evidence for the presumed relationship among *Barnhartia*, *Diclidanthera*, and *Moutabea*, and confirming their separation from *Eriandra*.

In summary, the phylogeny of the tribe, based on anatomical evidence, indicates that *Barnhartia*, *Diclidanthera*, and *Moutabea* are more closely related to one another than they are to *Eriandra*. In addition, *Barnhartia* and *Diclidanthera* are more closely related to each other than to *Moutabea*. These conclusions agree with the assessment (based on floral morphology) of van Royen and van Steenis (1952), except for their consideration of *Diclidanthera* as closely related to *Eriandra*.

The anatomical evidence supports several taxonomic conclusions. First, it seems quite clear that the genera of Moutabeae are all polygalaceous. For example, in both Moutabeae and other Polygalaceae, some genera have stems with similar types of anomalous growth. Both groups also possess solitary vessels with simple perforation plates, alternate intervascular pitting, and imperforate tracheary elements with bordered pits (Metcalfe & Chalk, 1950; Biswas, 1969). Leaves of both groups are similar in possessing unicellular or multicellular uniseriate hairs, epidermides with generally straight anticlinal walls, and generally anomocytic stomatal apparatuses (Metcalfe & Chalk, 1950). Crateriform extrafloral nectaries or glands are also distributed throughout the family. In my opinion, these anatomical features provide a basis for strong arguments against further usage of Diclidantheraceae to represent a group separate from Polygalaceae. This is especially true if, as in Metcalfe and Chalk (1950), *Barnhartia* is treated under Polygalaceae, since *Barnhartia* and *Diclidanthera* are practically indistinguishable anatomically.

A second taxonomic conclusion sustained by anatomical evidence is that the genera of Moutabeae are homogeneous enough to warrant being placed in a single tribe. However, it is not yet certain that anatomy would sub-

stantiate the tribal lines now drawn by taxonomists in the Polygalaceae. For example, Hutchinson (1967) and others place *Bredemeyera* Willd. and *Securidaca* L. in the tribe Polygaleae. Both of these are lianous genera with anomalous secondary growth very similar to that in Moutabeae (Müller, 1866; Crüger, 1850; Chodat, 1896; Schenck, 1893; Metcalfe & Chalk, 1950). Further anatomical study of these and other genera of Polygalaceae would be needed to test the tribal boundaries. If further study revealed that the Polygaleae and Moutabeae are too similar to be separated anatomically, the present morphologically based distinction between the tribes would be weakened. On the other hand, if further anatomical study revealed differences among members of the tribes, present tribal distinctions would be strengthened. It would be more likely that basic differences would be discovered in the leaves of the lianous genera than in the stems, since the structure of stems may reflect the peculiar mechanical and physiological demands of lianous habit rather than any genetic relationships.

Finally, my work bears out Perkins's (1907) exclusion of *Diclidanthera* from the Styracaceae, because the Styracaceae almost universally possess scalariform perforation plates and often have stellate hairs (Solereder, 1908), while *Diclidanthera* shows only simple perforation plates and uniseriate hairs.

ACKNOWLEDGMENTS

I thank Dr. William Louis Stern for his guidance and assistance with my research and with the subsequent writing of this paper. My thanks are also extended to Dr. James L. Reveal for suggesting the Moutabeae as a research subject and for obtaining herbarium sheets for study; to Dr. Leo J. Hickey, Smithsonian Institution, for help in interpreting leaf architecture in the Moutabeae; and to Dr. John J. Wurdack, Smithsonian Institution, for his continuing interest and advice. Thanks are also due to the following scientists and institutions throughout the world who provided specimens for this study: Dr. Pieter Baas, Rijksherbarium, Leiden; Dr. Alberta M. W. Mennega, Botanical Museum and Herbarium, Utrecht; Dr. Calvino Mainiera, Instituto de Pesquisas Tecnológicas, São Paulo, Brazil; Mr. John D. Brazier, British Forest Products Research Laboratory, Princes Risborough, England; Dr. Regis B. Miller, U. S. Forest Products Laboratory, Madison; Dr. Marga Teunissen-Werkhoven, Herbarium, Forest Service, Paramaribo; Mr. H. D. Ingle, Division of Forest Products, South Melbourne; and Dr. Richard A. Howard, Director, The Arnold Arboretum, Harvard University. I wish particularly to thank Dr. João Murça Pires, Instituto de Pesquisas e Experimentaçao Agropecuárias do Norte, for providing me with fluid-preserved specimens; and the Keeper, Royal Botanic Gardens, Kew, for supplying several prepared slides for my use. Special thanks are due my wife, Eloise, for assistance in all phases of my work.

LITERATURE CITED

AGARDH, J. G. 1858. Theoria systematis plantarum. xcvi + 404 pp. C. W. K. Gleerup, Lund.

ARNOTT, H. J. 1959. Leaf clearings. Turtox News **37:** 192–194.

AUBLET, J. B. C. F. 1775. Histoire des plantes de la Guiane françoise. Vol. 2. Pp. 678–682. P. Didot, London & Paris.

AYENSU, E. S. 1967. Aerosol OT solution — an effective softener of herbarium specimens for anatomical study. Stain Tech. **42:** 155, 156.

——— & W. L. STERN. 1964. Systematic anatomy and ontogeny of the stem in Passifloraceae. Contr. U. S. Natl. Herb. **34:** 45–73.

BAILEY, I. W. 1936. The problem of differentiating and classifying tracheids, fiber-tracheids, and libriform fibers. Trop. Woods **45:** 18–23.

———. 1953. The anatomical approach to the study of genera. Chron. Bot. **14:** 121–125.

——— & W. W. TUPPER. 1918. Size variation in tracheary cells: I. A comparison between the secondary xylems of vascular cryptogams, gymnosperms and angiosperms. Proc. Am. Acad. Arts **54:** 147–204.

BENTHAM, G. 1876. Styraceae. *In*: G. BENTHAM & J. D. HOOKER, Genera plantarum. Vol. 2. Pp. 666–671. L. Reeve & Co., London.

BISWAS, D. 1969. A study of xylem in the family Polygalaceae. Master's Thesis. Miami University. Oxford, Ohio. [Unpublished.]

CANDOLLE, A. DE. 1844. Styracaceae. *In*: Prodromus systematis naturalis regni vegetabilis. Vol. 8. Pp. 244–272. Fortin Masson, Paris.

CARLQUIST, S. 1961. Comparative plant anatomy. ix + 146 pp. Holt, Rinehart & Winston, New York.

CHALK, L., & M. M. CHATTAWAY. 1937. Identification of woods with included phloem. Trop. Woods **50:** 1–31.

CHENERY, E. M. 1948. Aluminium in the plant world. Kew Bull. 3: 173–183.

CHODAT, R. 1896. Polygalaceae. *In*: A. ENGLER & K. PRANTL, Die natürlichen Pflanzenfamilien. Vol. 3, part 4. Pp. 323–345. Wilhelm Engelmann, Leipzig.

Committee on Nomenclature, International Association of Wood Anatomists. 1957. International glossary of terms used in wood anatomy. Trop. Woods **107:** 1–36.

CRONQUIST, A. 1968. The evolution and classification of flowering plants. x + 396 pp. Houghton Mifflin Co., Boston.

CRÜGER, H. 1850. Einige Beiträge zur Kenntniss von sogenannten anomalen Holzbildungen des Dikotylenstammes. Bot. Zeit. (Berlin) 8: 161–171.

CUMBIE, B. G. 1960. Anatomical studies in the Leguminosae. Trop. Woods **113:** 1–47.

DEBARY, A. 1884. Comparative anatomy of the vegetative organs of the phanerogams and ferns. (Translated by F. O. BOWER & D. H. SCOTT.) xvi + 659 pp. Clarendon Press, Oxford.

DUBE, V. P. 1962. Morphological and anatomical studies in Polygalaceae and its allied families. Agra Univ. Jour. Res. Sci. **11:** 109–112.

EAMES, A. J., & L. H. MACDANIELS. 1947. An introduction to plant anatomy. ed. 2. xvii + 427 pp. McGraw-Hill Book Co., New York.

ENDLICHER, S. 1839. Genera plantarum. Pp. 741–745. Fr. Beck, Vienna.

ENGLER, A., & L. DIELS. 1936. Syllabus der Pflanzenfamilien. ed. 11. xlii + 419 pp. Gebrüder Borntraeger, Berlin.

——— & E. GILG. 1924. Syllabus der Pflanzenfamilien. eds. 9 & 10. xlii + 420 pp. Gebrüder Borntraeger, Berlin.

ERDTMAN, G. 1944. The systematic position of the genus *Diclidanthera* Mart. Bot. Not. **97:** 80–84.

———. 1952. Pollen morphology and plant taxonomy. xii + 539 pp. The Chronica Botanica Co., Waltham, Massachusetts.

ESAU, K. 1965. Plant anatomy. ed. 2. xx + 767 pp. John Wiley & Sons, New York.

FAHN, A. 1974. Plant anatomy. ed. 2. viii + 611 pp. Pergamon Press, New York.

FOSTER, A. S. 1944. Structure and development of sclereids in the petiole of *Camellia japonica* L. Bull. Torrey Bot. Club **71:** 302–326.

———. 1945. Origin and development of sclereids in the foliage leaf of *Trochodendron aralioides* Sieb. & Zucc. Am. Jour. Bot. **32:** 456–468.

———. 1946. Comparative morphology of foliar sclereids in the genus *Mouriria* Aubl. Jour. Arnold Arb. **27:** 253–271.

———. 1947. Structure and ontogeny of the terminal sclereids in the leaf of *Mouriria huberi* Cogn. Am. Jour. Bot. **34:** 501–514.

———. 1956. Plant idioblasts: remarkable examples of cell specialization. Protoplasma **46:** 184–193.

GILG, E. 1908. Die systematische Stellung der Gattung *Hoplestigma* und einiger anderer zweifelhafter Gattungen. Bot. Jahrb. **40**(Beibl. 93): 76–84.

GLEASON, H. A. 1926. Studies on the flora of northern South America. IX. Miscellaneous new species from British Guiana. Bull. Torrey Bot. Club **53:** 289–301.

GÜRKE, M. 1891. Styracaceae. *In*: A. ENGLER & K. PRANTL, Die natürlichen Pflanzenfamilien. Vol. 4, part 1. Pp. 172–180. Wilhelm Engelmann, Leipzig.

HEGNAUER, R. 1969. Chemotaxonomie der Pflanzen. Vol. 5. 506 pp. Birkhäuser, Basel.

HEIMSCH, C., JR. 1942. Comparative anatomy of the secondary xylem in the "Gruinales" and "Terebinthales" of Wettstein with reference to taxonomic grouping. Lilloa **8:** 83–198.

HESS, R. W. 1950. Classification of wood parenchyma in dicotyledons. Trop. Woods **96:** 1–20.

HICKEY, L. J. 1973. Classification of the architecture of dicotyledonous leaves. Am. Jour. Bot. **60:** 17–33.

HOLMGREN, P. K., & W. KEUKEN. 1974. Index herbariorum. Part 1. The herbaria of the world. ed. 6. Regnum Veg. **92:** 1–397.

HUTCHINSON, J. 1967. The genera of flowering plants. Vol. 2. 659 pp. Clarendon Press, Oxford.

JOHANSEN, D. A. 1940. Plant microtechnique. xi + 523 pp. McGraw-Hill Book Co., New York.

KRIBS, D. A. 1935. Salient lines of structural specialization in the wood rays of dicotyledons. Bot. Gaz. (Crawfordsville) **96:** 547–557.

LEWIS, W. H., & O. HERRERA-MACBRYDE. 1969. Family Polygalaceae. Part VI. Family 96. *In*: R. E. WOODSON, JR., R. W. SCHERY, *et al.*, Flora of Panama. Ann. Missouri Bot. Gard. **56:** 9–28.

LINDLEY, J. 1836. A natural system of botany. ed. 2. Pp. 226–228. Longman, Rees, Orme, Brown, Green, & Longman, London.

———. 1846. The vegetable kingdom. lxvii + 908 pp. Bradbury & Evans, London.

MACBRIDE, J. F. 1950. Polygalaceae Lindl. *In*: Field Mus. Nat. Hist., Bot. Ser. 13. Flora of Peru. Pt. 3(3): 9–28.

MARTIUS, C. F. P. VON. 1827. Nova genera et species plantarum, quas in itinere per Brasiliam annis 1817–1820. Vol. 2. Pp. 139–141. C. Wolf, München.

METCALFE, C. R., & L. CHALK. 1950. Anatomy of the dicotyledons. lxiv + 1500 pp. Clarendon Press, Oxford.

MIERS, J. 1861. Contributions to botany, iconographic and descriptive. Vol. 1. Pp. 213–221. Williams & Norgate, London.

MIQUEL, F. A. G. 1856. Ebenaceae. *In*: C. F. P. VON MARTIUS. Flora Brasiliensis. Vol. 7. Pp. 1–20. F. Fleischer, München & Leipzig.

MOHL, H. VON, & D. F. L. VON SCHLECHTENDAL. 1856. Ueber die Stellung der Pflanzengattungen *Moutabea* und *Diclidanthera* im natürlichen Systeme. Bot. Zeit. (Leipzig) **14:** 459–461.

MÜLLER, F. 1866. Ueber das Holz einiger um Desterro wachsenden Kletterpflanzen. Bot. Zeit. (Leipzig) **24:** 57–60.

O'DONELL, C. A. 1941. La posición sistemática de "Diclidanthera" Mart. Lilloa **6:** 207–212.

OORT, A. J. P. 1939. Polygalaceae. *In*: A. PULLE, Flora of Suriname. Vol. 2, part 1. Pp. 406–425. E. J. Brill, Leiden.

PERKINS, J. 1907. Styracaceae. *In*: A. ENGLER, Das Pflanzenreich **4**(241): 1–111. Wilhelm Engelmann, Leipzig.

PFEIFFER, H. 1925. Anatomische Betrachtung brasilianischer Hölzer. I. Beih. Bot. Centralbl. **41:** 165–178.

———. 1926. Das abnorme Dickenwachstum. *In*: K. LINSBAUER, Handbuch der Pflanzenanatomie. Bd. 9. Lieferung 15. xii + 268 pp. Gebrüder Borntraeger, Berlin.

PITTIER, H. 1942. Notas dendrológicas de Venezuela. Bol. Soc. Venez. Ci. Nat. **7:** 303–314.

RAO, T. A. 1951. Studies on foliar sclereids. A preliminary survey. Jour. Indian Bot. Soc. **30:** 28–39.

———. 1957. Comparative morphology and ontogeny of foliar sclereids in seed plants. I. *Memecylon* L. Phytomorphology **7:** 306–330.

RECORD, S. J. 1936. Classifications of various anatomical features of dicotyledonous woods. Trop. Woods **47:** 12–27.

——— & R. W. HESS. 1943. Timbers of the New World. xv + 640 pp. Yale Univ. Press, New Haven.

REICHENBACH, H. G. L. 1828. Conspectus regni vegetabilis. xiv + 294 pp. C. Cnobloch, Leipzig.

ROCK, B. N. 1972. The woods and flora of the Florida Keys: "Pinnatae." Smithson. Contr. Bot. **5:** 1–35.

ROYEN, P. VAN, & C. G. G. J. VAN STEENIS. 1952. *Eriandra*, a new genus of Polygalaceae from New Guinea. Jour. Arnold Arb. **33:** 91–95.

SCHENCK, H. 1893. Beiträge zur Biologie und Anatomie der Lianen. II. Beiträge zur Anatomie der Lianen. *In*: A. F. W. SCHIMPER, Botanische Mitteilungen aus den Tropen. V. Gustav Fischer, Jena.

SCHOLZ, H. 1964. Polygalaceae. *In*: A. ENGLER, Syllabus der Pflanzenfamilien. ed. 12. Bd. 2. Pp. 275, 276. Gebrüder Borntraeger, Berlin.

SOLEREDER, H. 1908. Systematic anatomy of the dicotyledons. (Translated by L. A. BOODLE & F. E. FRITSCH; revised by D. H. SCOTT.) Vols. 1, 2. Clarendon Press, Oxford.

SPRAGUE, T. A. 1940. Taxonomic botany, with special reference to the angiosperms. *In*: J. HUXLEY, ed. The new systematics. Pp. 435–454. Clarendon Press, Oxford.

——— & N. Y. SANDWITH. 1932. *Barnhartia floribunda* Gleason. Hooker's Icon. Pl. Ser. 5. **2**(3): *Tab. 3172.* Pp. 1–3.

STAFLEU, F. A. 1967. Taxonomic literature. Regnum Veg. **52:** 1–556.

STERN, W. L. 1967. Index xylariorum. Regnum Veg. **49:** 1–36.

———, E. M. SWEITZER, & R. E. PHIPPS. 1970. Comparative anatomy and systematics of woody Saxifragaceae. *Ribes.* Jour. Linn. Soc. Bot. **63**(Suppl. 1): 215–237.

TAMOLANG, F. M., R. R. VALBUENA, J. A. MENIADO, & B. C. DE VELA. 1963. Standards and procedures for descriptions of dicotyledonous woods. Forest Prod. Res. Inst. Bull. 2. iii + 15 pp. College, Laguna, Philippines.

TIPPO, O. 1941. A list of diagnostic characteristics for descriptions of dicotyledonous woods. Trans. Ill. Acad. **34:** 105, 106.

TUCKER, S. C. 1964. The terminal idioblasts in magnoliaceous leaves. Am. Jour. Bot. **51:** 1051–1062.

WETTSTEIN, R. 1935. Handbuch der systematischen Botanik. ed. 4. iv + 1152. Franz Deuticke, Leipzig.

DEPARTMENT OF BOTANY
UNIVERSITY OF MARYLAND
COLLEGE PARK, MARYLAND 20742

EBENACEAE HARDY IN TEMPERATE NORTH AMERICA [1]

STEPHEN A. SPONGBERG

EBENACEAE Gürke in Engler & Prantl, Nat. Pflanzenfam. IV. 1: 153. 1891, nom. cons.

(EBONY FAMILY)

Evergreen or deciduous trees and shrubs, usually with very hard, blackish wood and watery sap. Leaves simple, alternate or rarely opposite or whorled, exstipulate, mostly with entire margins, the venation pinnate. Flowers actinomorphic, imperfect (and the plants dioecious or sometimes monoecious), or sometimes occasional flowers perfect (and the plants polygamous or polygamodioecious); staminate flowers usually in few-flowered, axillary, cymose inflorescences; carpellate flowers axillary, usually solitary. Calyx synsepalous, articulated at base, 3–7-lobed, often accrescent in age. Corolla sympetalous, 3–7-lobed, the lobes usually contorted, imbricate (or rarely valvate) in bud. Stamens usually 2 or 3 times the number of corolla lobes, epipetalous (or rarely hypogynous), in 2 or more whorls, the filaments free or connate, the anthers 2-loculate; in carpellate flowers the androecia reduced to staminodia or absent. Gynoecium syncarpous, the styles connate for all or a portion of their length; ovary superior, 2–16 (–20)-locular, each locule with 1 or 2 pendulous, anatropous, bitegmic ovules; in staminate flowers the gynoecia vestigial or absent. Fruit a berry, often succulent, usually subtended by the persistent calyx. Seeds with thin coats, the straight or slightly curved embryos with foliaceous cotyledons, embedded in copious cartilaginous or sometimes ruminate endosperm. (Guaiacanae Jussieu, Diospyraceae Novak; including Lissocarpaceae Gilg; excluding Onocatheaceae Kobuski ex Airy Shaw.) TYPE GE-

[1] This treatment of the Ebenaceae is the fourth contribution in a series of treatments of cultivated ligneous plants, the preparation of which is a project of the Arnold Arboretum of Harvard University, and the purpose of which is to provide a modern, accurate account of the woody plants encountered in cultivation in the cooler temperate regions of North America. It is hoped that these treatments will eventually form the basis of a new manual of cultivated woody plants. The first paper in this series was published in the Journal of the Arnold Arboretum **56**: 1–19. 1975. Reference should be made to the introductory paragraphs of that paper for matters concerning area covered, taxa included, and the general philosophy of these treatments.

Special thanks and gratitude are extended to the Director and trustees of the Stanley Smith Horticultural Trust for a grant that has made possible the illustrations to accompany these treatments. The illustrations are the careful work of Robin S. Lefberg and were prepared from living and alcohol-preserved specimens collected in the Arnold Arboretum and at the Henry Foundation for Botanical Research, Gladwyne, Pennsylvania.

For their contributions of time and advice and encouragement, I am indebted to my colleagues on the staff of the Arnold Arboretum and to many botanical and horticultural friends and colleagues. Particular thanks are extended to my wife, Harmony, to Dr. J. C. McDaniel, Mr. J. Witt, and Dr. B. G. Schubert. S. A. S.